

For Reference

NOT TO BE TAKEN FROM THIS ROOM

Ex LIBRIS
UNIVERSITATIS
ALBERTAE NSIS





Digitized by the Internet Archive
in 2019 with funding from
University of Alberta Libraries

<https://archive.org/details/Labelle1982>

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Marc Labelle
TITLE OF THESIS SOME ASPECTS OF THE POPULATION DYNAMICS
 OF THE REDLIP BLENNY, *OPHIOBLENNIUS*
 ATLANTICUS (TELEOSTEI: BLENNIIDAE)
DEGREE FOR WHICH THESIS WAS PRESENTED Master of Science
YEAR THIS DEGREE GRANTED Fall 1982

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

THE UNIVERSITY OF ALBERTA

SOME ASPECTS OF THE POPULATION DYNAMICS OF THE REDLIP
BLENNY, *OPHIOBLENNIUS ATLANTICUS* (TELEOSTEI: BLENNIIDAE)

by



Marc Labelle

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Master of Science

Department of Zoology

EDMONTON, ALBERTA

Fall 1982

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled SOME ASPECTS OF THE POPULATION DYNAMICS OF THE REDLIP BLENNY, *OPHIOBLENNIUS ATLANTICUS* (TELEOSTEI: BLENNIIDAE) submitted by Marc Labelle in partial fulfilment of the requirements for the degree of Master of Science.

abstract

The redlip blenny, *Ophioblennius atlanticus macclurei*, is a common shallow water reef fish found in the western central Atlantic from North Carolina to Venezuela. Adults of both sexes hold permanent territories. The sex ratio of the species has been determined to be 1:1. Reproductive periodicity in redlip blennies is correlated with the full moon phase of the lunar cycle. Both polygamy and polyandry were observed in the population. Body size, nest emplacement and nest volume play an important role in mate selection. Spawning occurs mostly during the early morning hours (0600 to 0900 hrs). Demersal eggs are maintained and cared for by the male until hatching occurs. Although reproduction in the species is a year round phenomenon, reproductive activity is maximal during March-April and minimal from September to November. Fecundity increases exponentially with length, and maximum fecundity in *O. atlanticus* is described by the equation;

$$F = 0.08710 L^{2.39}$$

An account is given of embryogenesis in *O. atlanticus*. The incubation period was determined to be 96-100 hours at 29° C. A description of the morphological and behavioral features of the early life history stages is provided. Based on data from an ichthyoplankton survey, information on the morphology and growth rates of the larval stages was obtained. Redlip blenny larvae have a pelagic existence of six weeks which is carried out mostly over nearshore and

inshore waters. During this period larvae grow at an overall rate of 0.91 mm per day. Large larvae (40-46mm TL) settle in the adult habitat and undergo metamorphosis within 7 days. A seasonal peak in recruitment occurs during mid summer (June-July) but no recruits were observed in August. It is hypothesized that outflow of the Amazon river has a strong influence on hydrographic conditions around Barbados which in turn may interfere with year round recruitment. The redlip blenny is adapted to its unpredictable environment and can therefore maintain its numerical abundance in its habitat.

ACKNOWLEDGEMENTS

This thesis is dedicated to Wendy Nixon, whose love and compassion have taught me a great deal and have helped me in completing this work. I also wish to thank Dr. J.R.Nursall for providing financial (NSERC Operating Grant A-2071), technical and moral support. I am grateful to Lauren Turner for her support and cooperation during the 1980 field season. Sincere thanks to Diane Hollingdale for her contributions as an illustrator. Finally I am most grateful to my parents for their understanding and encouragement without which I could have neither undertaken nor completed this work. The use of the facilities at the Bellairs Research Institute of McGill University was appreciated.

| Chapter | Table of Contents | Page |
|---------|--|------|
| 1. | INTRODUCTION | 1 |
| 2. | DESCRIPTION OF STUDY SITE | 3 |
| 3. | MATERIALS & METHODS | 9 |
| 4. | MATE SELECTION | 10 |
| 4.1 | Materials and methods | 10 |
| 4.1.1 | Nest contents | 10 |
| 4.1.2 | Mate selection | 11 |
| 4.2 | RESULTS | 12 |
| 4.2.1 | Nest contents | 12 |
| 4.2.2 | Mortality rates | 13 |
| 4.2.3 | Factors influencing #eggs/nest | 14 |
| 4.2.4 | Mating Success | 16 |
| 4.2.5 | Female choice | 17 |
| 4.2.6 | Male choice | 20 |
| 4.3 | DISCUSSION | 22 |
| 5. | REPRODUCTIVE ACTIVITIES | 27 |
| 5.1 | DEFINITIONS | 27 |
| 5.2 | Reproductive Behavior | 27 |
| 5.2.1 | Materials and methods | 27 |
| 5.2.2 | Results | 28 |
| 5.3 | Reproductive Periodicity | 38 |
| 5.3.1 | Materials and Methods | 38 |
| 5.3.2 | Results | 39 |
| 5.4 | DISCUSSION | 42 |
| 6. | REPRODUCTIVE SEASONALITY AND PERIODICITY | 47 |
| 6.1 | MATERIALS & METHODS | 47 |

| | | |
|-------|--|-----|
| 6.2 | RESULTS | 47 |
| 6.3 | DISCUSSION | 59 |
| 7. | REARING EXPERIMENTS | 66 |
| 7.1 | MATERIALS AND METHODS | 66 |
| 7.2 | RESULTS | 69 |
| 7.2.1 | Embryonic features of <i>O.atlanticus</i> | 69 |
| 7.2.2 | Embryogenesis in <i>O.atlanticus</i> | 70 |
| 7.2.3 | Larval morphology (part 1) | 74 |
| 7.2.4 | Behavioral observations of redlip blenny larvae | 84 |
| 7.2.5 | Feeding experiments | 90 |
| 7.3 | DISCUSSION | 95 |
| 8. | ICHTHYOPLANKTON SURVEY | 98 |
| 8.1 | MATERIALS & METHODS | 99 |
| 8.1.1 | Offshore tows | 99 |
| 8.1.2 | Nearshore tows | 102 |
| 8.1.3 | Additional sampling | 103 |
| 8.1.4 | Processing & Identification | 104 |
| 8.2 | RESULTS | 108 |
| 8.2.1 | Larval Morphology (part II) | 108 |
| 8.2.2 | Larval distribution and abundance | 113 |
| 8.3 | DISCUSSION | 118 |
| 9. | RECRUITMENT | 127 |
| 9.1 | Materials & Methods | 128 |
| 9.1.1 | Investigation I | 128 |
| 9.1.2 | Investigation II | 131 |
| 9.1.3 | Investigation III | 133 |

| | | |
|-------|---------------------------|-----|
| 9.2 | RESULTS | 135 |
| 9.2.1 | Investigation I | 135 |
| 9.2.2 | Investigation II | 137 |
| 9.2.3 | Investigation III | 142 |
| 9.3 | DISCUSSION | 149 |
| 10. | DEMOGRAPHIC STUDIES | 161 |
| 10.1 | MATERIALS & METHODS | 161 |
| 10.2 | RESULTS | 162 |
| 10.3 | DISCUSSION | 165 |
| 11. | CONCLUSION | 171 |
| 12. | LITERATURE CITED | 175 |
| 13. | APPENDIX | 184 |

List of Tables

| TABLE | DESCRIPTION | PAGE |
|-------|--|------|
| 1. | Male mating success vs. female fecundity | 18 |
| 2. | Female nesting activity | 29 |
| 3. | Male nesting activity | 32 |
| 4. | Analysis of male nesting time | 34 |
| 5. | Description of <i>O.atlanticus</i> larva (24 hours old) | 82 |
| 6. | Ichthyoplankton Survey Data | 105 |
| 7. | Description of <i>O.atlanticus</i> larvae (part II) | 112 |
| 8. | Distribution and abundance of <i>O.atlanticus</i> larvae. | 114 |
| 9. | Details of redlip blenny captures | 136 |
| 10. | Description of <i>O.atlanticus</i> larvae (part III) | 140 |
| 11. | Description of <i>O.atlanticus</i> larvae (part IV) | 148 |
| 12. | Fishes captured on isolated coral head | 150 |

List of Figures

| FIGURE | DESCRIPTION | PAGE |
|--------|--|------|
| 1. | Geographical position of Barbados in Western Central Atlantic | 5 |
| 2. | Location of major study site | 7 |
| 3. | Distribution of redlip blenny nests | 21 |
| 4. | Body size of male vs. female (in mating pairs) | 23 |
| 5. | Frequency distribution of nesting times in <i>O.atlanticus</i> | 31 |
| 6. | <i>O.atlanticus</i> nesting behavior through time | 36 |
| 7. | Number of nest-guards in transect through time | 41 |
| 8. | Annual tidal regime of Barbados (1981) | 44 |
| 9. | Oogenesis in <i>O.atlanticus</i> through time | 50 |
| 10. | Gonadal state of female redlip blennies through time | 53 |
| 11. | Seasonal GSI of female redlip blennies | 55 |
| 12. | Seasonal fecundity in <i>O.atlanticus</i> | 58 |
| 13. | Annual female gonadal change (1981) | 61 |
| 14. | Diagram of the aquarium | 67 |

| | |
|--|-----|
| 15. <i>O.atlanticus</i> larva (24 hours old) | 79 |
| 16. <i>O.atlanticus</i> larva (5.86 mm TL) | 110 |
| 17. Position of experimental enclosures at Heron Bay reef | 132 |
| 18. <i>O.atlanticus</i> larva (19.64 mm TL) | 139 |
| 19. <i>O.atlanticus</i> post-larva. | 147 |
| 20. Catches of <i>O.atlanticus</i> larvae at study site | 153 |
| 21. Number of redlip blennies in transect A vs. time (1980-81) | 164 |
| 22. Number of redlip blennies in transect B vs. time (1981) | 166 |
| 23. Salinity and temperature profile of surface waters at Barbados (1980-81). | 186 |

List of Plates

| PLATE | DESCRIPTION | PAGE |
|-------|--|------|
| 1. | <i>O.atlanticus</i> embryos; 8 and 48 hours old | 72 |
| 2. | <i>O.atlanticus</i> embryos; 52 and 58 hours old | 73 |
| 3. | <i>O.atlanticus</i> embryos; 74 and 92 hours old | 75 |
| 4. | <i>O.atlanticus</i> embryo at hatching | 76 |
| 5. | Underwater enclosures at Heron Bay | 130 |
| 6. | Author sampling fauna from isolated coral head | 134 |
| 7. | <i>O.atlanticus</i> post-larva and pre-juvenile | 143 |
| 8. | Juvenile and pre-juvenile <i>O.atlanticus</i> | 144 |

1. INTRODUCTION

The redlip blenny, *Ophioblennius atlanticus macclurei* (Silvester), is a small herbivorous reef fish which holds permanent territories on coral reefs in shallow waters (Nursall 1977). It has been characterized as one of the most abundant fishes on West Indian reefs (Randall 1968). Although it is of no commercial value in itself (Fisher 1978), as a primary consumer it does contribute to the support of a large number of predators which are commercially harvested. In the eastern Caribbean, almost all the fishing effort is directed towards exploitation of the reef population (Munro 1976). In these areas, approximately 180 species of reef fishes and invertebrates taken from the reefs, are known to be marketed by fisherman.

After a close examination of the fisheries potential of coral reef environments, Stevenson & Marshall (1974) concluded; "Reference to suitable management regulations brings up the need for fundamental fishery biology information to accompany development efforts. First and foremost, we need such basic facts as harvest statistics, population estimates related to supporting environments, growth rate data, reproduction-recruitment data, etc.".

An investigation into the population dynamics of the redlip blenny, *O. atlanticus* was undertaken with the object of acquiring background information on such processes. Such information is of prime importance to biologists since I believe the redlip blenny plays a vital role in the

structure and composition of the shallow water coral reef communities of Caribbean islands. Furthermore, many of its life history stages are under the influence of the same environmental factors affecting other reef fishes.

The topics discussed in this study include: mate selection, reproductive behavior, spawning periodicity, fecundity analysis, ontogeny, larval morphology, larval behavior, larval distribution, recruitment and population stability.

Springer (1962) reviewed the genus *Ophioblennius* and described the morphology of the redlip blenny. Nursall (1977) gave a detailed account of territoriality in this species. Marraro (1978) carried out an investigation into the life history and behavioral ecology of *O.atlanticus*. This study complements these previous investigations.

The studies reported here took place along the St.James coast of Barbados. All field work was carried out during May to September 1980, and January to September 1981.

2. DESCRIPTION OF STUDY SITE

Situated approximately at latitude $13^{\circ} 04'$ north and longitude $59^{\circ} 37'$ west, Barbados is 140 km east of the island chain marking the eastern boundary of the Caribbean sea and 250 km northeast of Trinidad (Fig.1). It is a relatively small coral capped island (34 km X 22 km) with its longest axis lying north to south.

Because of its geographical position, meteorological and oceanographic conditions around Barbados are fairly constant. Surface sea temperature ranges from 26.0° C. (early winter) to 29.5° C. (late summer), while salinity in surface layers fluctuates from 33.5 ‰ (September-October) to 36.5 ‰ (February-March, Sander & Steven 1973).

All studies reported here took place on the west coast of Barbados. Plankton tows were conducted over inshore and offshore waters along this coast. All other data were obtained from the nearshore fringing reefs adjacent to the Bellairs Research Institute in St. James (Fig. 2). This reef is approximately 250 m long, 150 m wide, and ranges from one to 8 m in depth.

Lewis (1960) described the topography and coral communities along the St-James Coast of Barbados and recognized three zones of inshore fringing reefs; Reef Flat Zone, Reef Crest Zone and the Seaward Slope.

A detailed description of the Reef Crest Zone was given by Marraro (1978) and is repeated here. The Reef Crest Zone is the climax zone of the living reef. The basic features of

FIGURE 1

GEOGRAPHICAL POSITION OF BARBADOS
IN WESTERN CENTRAL ATLANTIC
(after Powles 1975)

Dashed line represents the 200 m (depth) contour line.

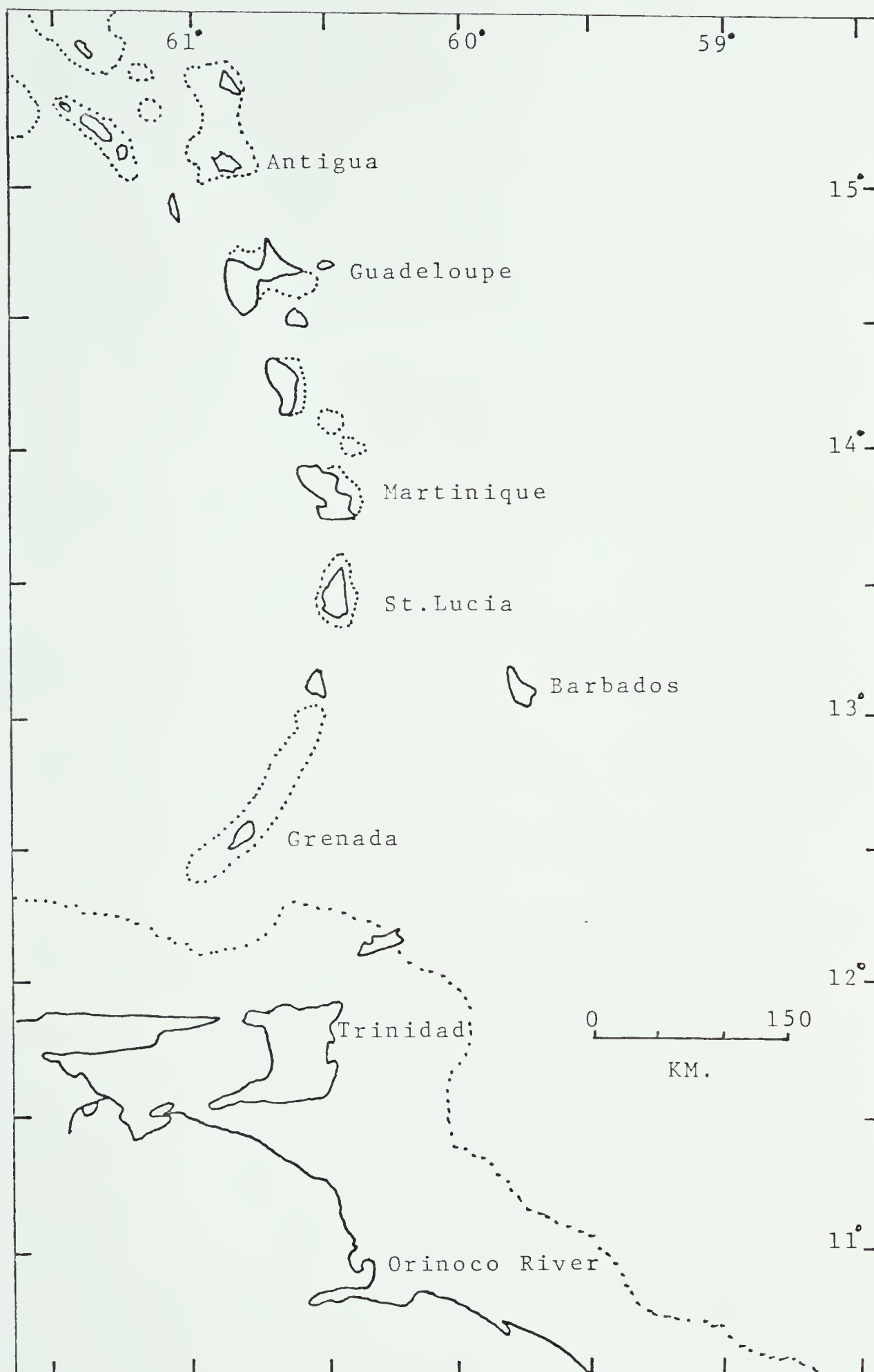
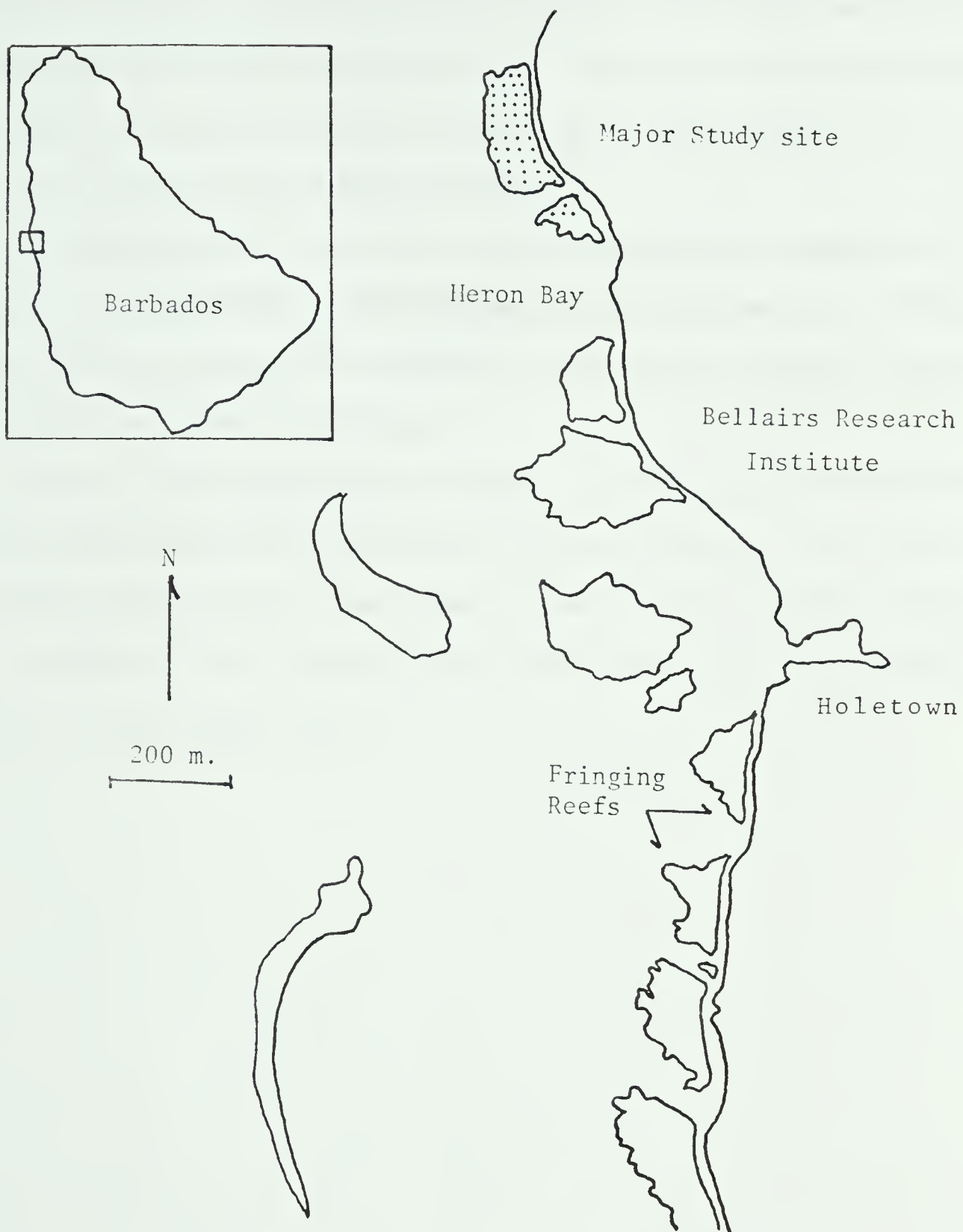


FIGURE 2

LOCATION OF MAJOR STUDY SITE



this zone include spurs or ridges which project outward toward the sea. Irregular winding valleys run between the ridges. The spurs lie perpendicular to the shore and have an irregular outline. The surface of the zone is characterized by dead coral rock which is secondarily encrusted with *Porites porites* and *P. astreoides*.

The dominant corals and chief structural elements of this zone are *Montastrea annularis* and *Siderastrea siderea*. Other corals which are abundant in this zone are *Millepora* sp. and *Montastrea cavernosa*.

Most field observations were carried out on the Reef Crest Zone where *O. atlanticus* is most abundant. This species has been observed on the inner areas of the seaward slope up to a depth of 8 m, but most of the population is found at a depth of less than 4 m.

3. MATERIALS & METHODS

Most information on the materials and methods used in the different investigations of this study is given at the beginning of each chapter. Only a brief account of the general methodology is provided here.

Field observations were conducted through the use of mask, snorkel and fins. All observations were recorded with a pencil on a hard plastic slate. Direct observation totaled approximately 300 hours. Sampling was mostly done by SCUBA. Individual fishes were killed with a small hand held spear. Eggs were collected with a hammer and chisel. Recruits and juveniles were obtained using Rotenone squeezed out of a hot water bottle.

A large, 1200 l, hexagonal aquarium was used to monitor egg and larval development. Pictures of the early life history stages of the redlip blenny were obtained using a WILD M5 microscope coupled to a WILD MPS 15/11 microphotographic set-up.

Redlip blenny larvae were collected over inshore and offshore waters. Sampling gear consisted of a 3.5 m long plankton net (mesh size 1.1 mm) with a large, square mouth (1.0 m²). During inshore tows, the net was towed behind a 5 m boat powered by a 25 hp. engine. The Bellairs Research Institute vessel "Martlet" was used to tow the same net over offshore waters.

4. MATE SELECTION

Marraro (1978) provided a detailed description of several reproductive activities in *O.atlanticus*. These included nest-selection and preparation, male and female pre-spawning activities and spawning sequence and behavior. No information was recorded on the process of mate selection, mating success or nest contents. During the present investigation, several observations on these processes, were recorded and are reported here.

4.1 Materials and methods

4.1.1 Nest contents

During the 1980 season, I would swim up to a coral head in the surge zone and anchor myself to the substrate. A redlip blenny within visual range (3 to 5 m) would be randomly selected. First an activity budget of the individual would be recorded¹. Then the territory patrolled by the individual during the previous 15 minutes, and the succeeding 30 minutes would be delineated by driving 8 to 10 red nails into the substrate.

During the following reproductive period, I would successively visit the marked territories and select redlip blennies exhibiting nest-guarding behavior². I would then record the activity budget of the fish, measure the area of

¹See section 5.2.1 for details

²As defined in section 5.2.2

the territory, the position of the nest on the coral head and in relation to the surface (at low tide), and record other characteristics of the nest that were readily apparent. The male would then be killed with a hand-held spear and the eggs obtained from the nest by cutting the walls of the crevice with a chisel. Before leaving, I would record the approximate size of the nest (in cm^3) with a ruler. In the lab, the sex of the fish was verified, its size measured to the nearest 0.1 mm, and the total number of eggs per nest determined by direct visual count using a dissecting microscope. The respective stage of development of each egg was determined by reference to the information obtained during rearing experiments (see section 7.2.2). During the 1981 field season, the procedure was similar but, due to time constraints, no measurements were made of territory size and nest emplacement.

4.1.2 Mate selection

Extensive observations on the pre-spawning interactions of redlip blennies were done during the early morning hours (0600-0830) throughout the reproductive periods of May, June and July 1981. I would observe the behavior of the fishes by floating passively at the surface in shallow water above the reef, with a mask, fins and snorkel. All behavioral sequences pertaining to reproductive activities were recorded on plastic paper or on a plastic slate. During this period, every pair of redlip blenny observed in the process

of spawning was killed with a hand held spear. These fishes were then placed in a plastic bag and brought back to the lab where they were sexed and measured to the nearest 0.1 mm. Before leaving the spawning site, I would check for the presence of eggs inside the nest.

4.2 RESULTS

4.2.1 Nest contents

A total of 67 nests were opened during the 1980-1981 season. The presence of eggs inside the nest corresponded (timewise) to that predicted from the behavioral analysis (see section 5.2.2). Typically, the nests contained eggs during the reproductive period (FM-7 to FM+7)³, and were empty during the non-reproductive period. I observed that most nests contained eggs at different developmental stages; the early or young stage (up to 30 hours old), the intermediate stage (up to 55 hours old) and the advanced stage (up to 80 hours old). The total number of eggs per nest ranged from 0 to 11490.

The presence of several broods of eggs⁴ inside a nest can be explained by the fact that redlip blennies spawn repeatedly during the reproductive period.

The number of different broods contained per nest ranged

³From 7 days before full moon, to 7 days after full moon

⁴ Defined as the number of batches of eggs of different development stages found inside a nest.

from one to three. In only two cases were four broods observed inside a nest, but in both cases, two of those four broods belonged to the intermediate stage as the eggs had been laid only a few hours apart.

4.2.2 Mortality rates

It was first believed that estimates on mortality rate of eggs could be obtained from noting the difference in the number of eggs in each brood or the amount of empty space within the area occupied by each brood of eggs. After a thorough examination of several nest contents, it was concluded that such data did not provide enough evidence to make such estimates.

Any inference about egg mortality during the incubation period therefore, stems from visual observations of nests in the field. Only one such observation is worth reporting here.

On August 2nd, 1980, while patrolling a transect, I noticed that a redlip blenny guarding some eggs, sustained heavy losses in the total number of eggs incubating in his nest. The surface occupied by the eggs in his nest was reduced from an initial surface area of 21 cm² to 8 cm² within a period of 24 hours. These eggs were in a very early stage of development and were definitely not ready to hatch. This egg patch had been laid on the external surface of fire coral, close to the surface of the water (3 cm below the surface at low tide). Several factors are proposed to

account for such heavy losses (60 %): high light intensity, increased exposure to predation, or failure of fertilization because of the very strong surge in that area of the water column. That such mortality is typical for redlip blennies is doubtful, as parental care is generally believed to decrease mortality during the incubation period. Further investigations are required to determine the average rates of mortality and the factors responsible for mortality during the incubation period.

4.2.3 Factors influencing #eggs/nest

Due to the incubation time (96 hours at 29° C.), it is theoretically possible for a male to have a nest containing four different broods at any one time. However, in almost all cases, only a maximum of three broods were observed inside a nest. Therefore, I believe that males may invariably 'prefer' to guard the eggs of a maximum of three females at any one time. More investigations are required to determine the exact nature of the constraints inducing such limitations.

The sampling technique used in this investigation does interrupt the reproductive activity of the male. It is not possible therefore to say with certainty whether or not what is observed inside the nest (in terms of total number of broods or eggs) is a clear representation of the actual reproductive potential for that male.

Nevertheless various biotic and abiotic parameters were

tentatively correlated. When considering the data on all nests (those containing one, two or three broods), no significant correlation ($r < 0.4$) was found to exist between the following features: Total number of eggs per nest, male body size, nest volume, territory size and territory emplacement.

In the present investigation, it was assumed that 'full' nests (i.e. those containing three broods of eggs) would best represent the reproductive potential of the guarding male, since at this stage, interference with any ongoing process is reduced. When using only the data on 'full' nests, the following relationships⁵ were observed:

| | | | |
|-----------|--------|--------|----------|
| Log(T.L.) | Versus | Log(E) | $r=0.71$ |
| N.V. | Versus | E. | $r=0.88$ |
| S.L. | Versus | N.V. | $r=0.57$ |

where:

T.L.= Total length of the resident male (mm)

S.L.= Standard length of the resident male (mm)

N.V.= Nest volume (in cm^3)

E.=Total number of eggs per nest

This clearly indicates that the number of eggs found in the nests of males during the reproductive period is a function of the size of the male and the volume of its nest.

A multiple regression analysis was done to account for the effects of both factors (body size and nest volume) on

⁵ Based on the pooled data of June 1980-81 and July 1981.

the egg content of the nest. The regression equation obtained was:

$$E = -1512 + 67.9(S.L) + 7.73 (N.V) \quad (r=0.875 \quad n=14) ^6$$

No relationship was found between the total number of eggs and the male's territory size, nor between body size of males and their territory size. Although Nursall(1977) suggested that territory size is related to body size in *O.atlanticus*, it has been proposed (Nursall, pers. comm.) that such relationship only occurs under conditions of high population density. Since all specimens were obtained randomly without considering the presence or absence of neighbours, this may account for the lack of a significant relationship between the two factors. Further investigation is required to evaluate the effects of territory quality and size on the number of eggs per nest.

4.2.4 Mating Success

Data on nest contents during June and July 1980-81 can be used to account in part for the mating success of males. The fecundity of females may be calculated from the relationships proposed in section 6.2. Since males tend to mate with females of equal body size (see section 4.2.6), the potential number of females each male may mate with can

⁶Only data from June 1980-81 was used

be calculated. This information is presented in Table 1 and suggests that in all cases in which three broods were found in the nest, the males must have spawned with a minimum of two females. This confirms earlier observations that polygyny occurs in *O. atlanticus*. Evidence of polyandry in redlip blennies has also been obtained in the present investigation during field observations.

For reasons outlined earlier, nests containing one or two broods were not considered to provide information on mating success. However, I assume that some males guarding one or two broods of eggs have reached their reproductive potential. Further investigation is required to determine factors responsible for the lack of success of such males.

4.2.5 Female choice

During the spawning period, females leave their territory to search for males that are in reproductive conditions. Although several neighboring males may be ready to mate, females do not appear simply to distribute their eggs randomly or uniformly among the nests. Rather they appear to be strongly attracted by certain males. It is common to observe many females aggregating at the border of a male's territory, while few or none will aggregate at a neighbor's territory. Up to six females have been observed to aggregate at the perimeter of a single male territory (Marraro 1978). In order to determine the factors which may influence a female's choice, further attention was directed

TABLE 1

MALE MATING SUCCESS VS. FEMALE FECUNDITY

| #EGGS/NEST | T.L (male) (mm) | FECUNDITY eggs/female (*) | # MATES (potential) |
|------------|-----------------------|---------------------------------|------------------------|
| 1638 | 64.0 | 1124 | 1.46 |
| 3374 | 72.6 | 1649 | 2.05 |
| 8313 | 79.9 | 2206 | 3.77 |
| 2490 | 69.0 | 1413 | 1.76 |
| 11490 | 88.3 | 2990 | 3.84 |
| 4994 | 81.1 | 2309 | 1.73 |
| 5218 | 82.3 | 2414 | 2.16 |
| 9794 | 76.2 | 1910 | 5.13 |
| 6780 | 79.9 | 2206 | 3.07 |
| 3900 | 83.5 | 2522 | 1.55 |

* Calculated fecundity of a female the same size as the male.

at the pre-spawning behavior of males and females.

On a few occasions during the early morning hours (0600 to 0830) of days preceding the reproductive period, female blennies were observed 'visiting' the nests of males. While the male was simply positioned near the crevice, the female would enter the nest, remain up to 15 seconds inside and leave the nest without actually depositing any eggs. I was intrigued by such interactions since male blennies normally respond to such intrusions with aggressive displays and actions, except during the reproductive period when they permit females to enter the nest to spawn.

Since, at the time of these observations, I was mostly concerned with the male behavior, the visiting females were never followed to determine whether or not they visited other nests. There is no evidence to suggest that females only visit a single nest, therefore this action is not recognized as necessarily leading to spawning in all nests visited.

The above observations suggest that females may actually estimate the quality of each nest when choosing a mate. There is no way to determine with certainty what factors are of prime importance in affecting female choice. However, further information on the factors influencing female selection can be obtained by analyzing the mating success of males.

One potential indicator of male mating success lies in the number of eggs contained in his nest during the

reproductive period. Evidence provided from the analysis of nest contents (see section 4.2.3) strongly suggests that the body size of males and the size of its nest, are important factors influencing the total number of eggs found in each nest. Thus, it is possible that females prefer males of a certain size occupying nests of certain dimensions.

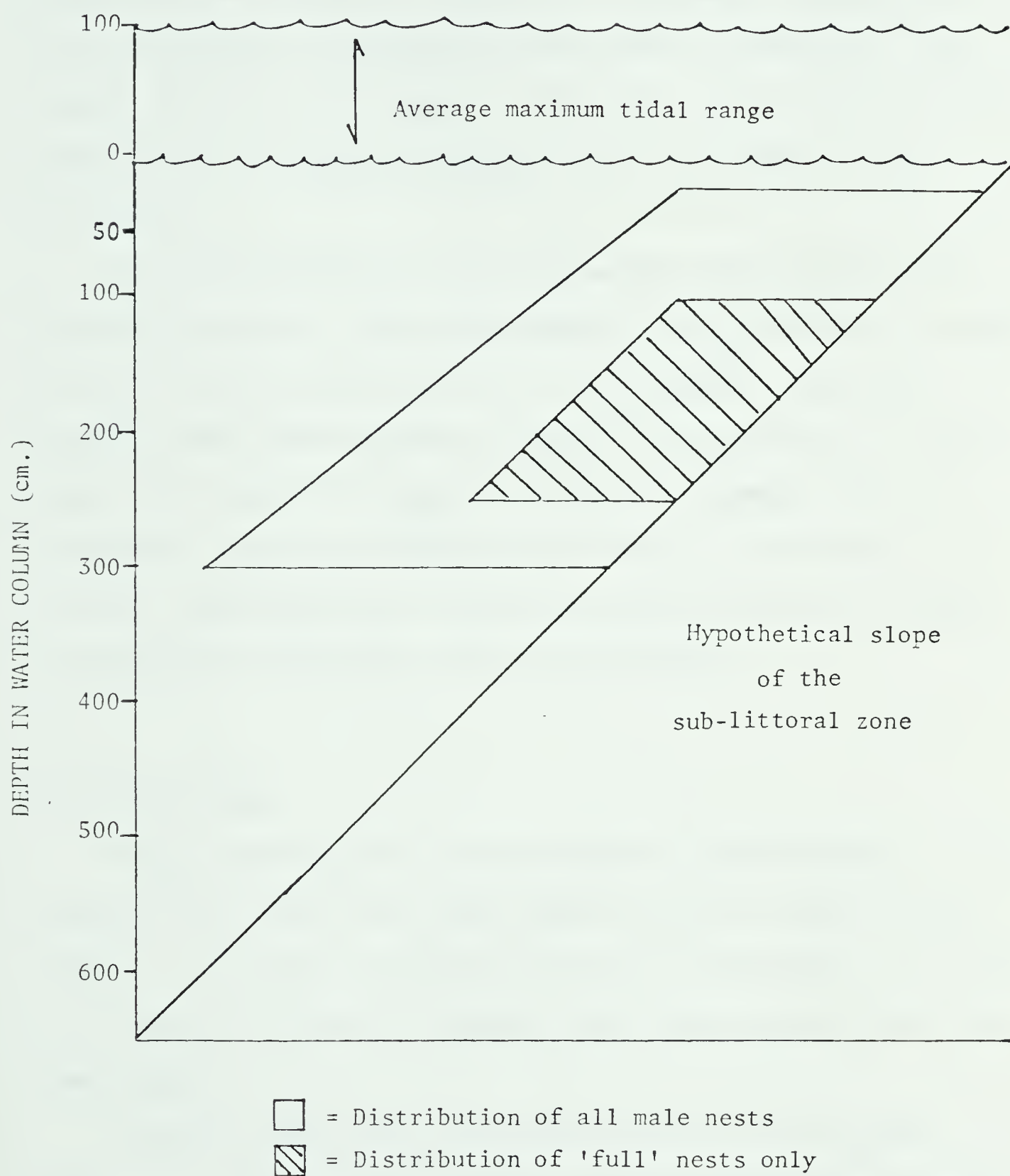
The number of broods contained in a nest is also informative in this regard. Empirical evidence obtained during 1980 on the distribution of nests, suggests that those nests containing three broods of eggs were not distributed in patterns similar to those of other nests containing one or two broods. Figure 3 shows that full nests are not as widely spread as all nests in the water column. This suggests that females may prefer nests located at a certain position in the water column. The position of full nests, in regard to the bottom substrate (or nest elevation), is no different than that of other nests and therefore appears to play no role in attracting females. A list of the principal factors (other than depth) which can account for the desirability of the nests cannot be proposed at this stage.

4.2.6 Male choice

Once the females have been attracted to the territory of a certain male, the male himself selects the female he will mate with. The typical behavior exhibited by the male in such circumstances has been described by Marraro (1978): "

FIGURE 3

DISTRIBUTION OF REDLIP BLENNY NESTS



If the male is ready to spawn, he will leave the nest, dorsal and anal fins erect, and will approach the female. When the male reaches the female, he will 'peck' her on the head and then return to the nest. The female responds to this action by following the male back to the nest. The female then lays her eggs in the nest." The male does not spawn with all females aggregating at the edge of his territory.

It was observed during preliminary observations of breeding activity, that both members of a mating pair seemed to be of similar body size. For this reason, males and females seen spawning were killed for examination. Figure 4 shows that there is a good correlation between the size (standard length) of the male and that of the female ($r = 0.926$), indicating that the male's choice may be strongly influenced by the body size of the female.

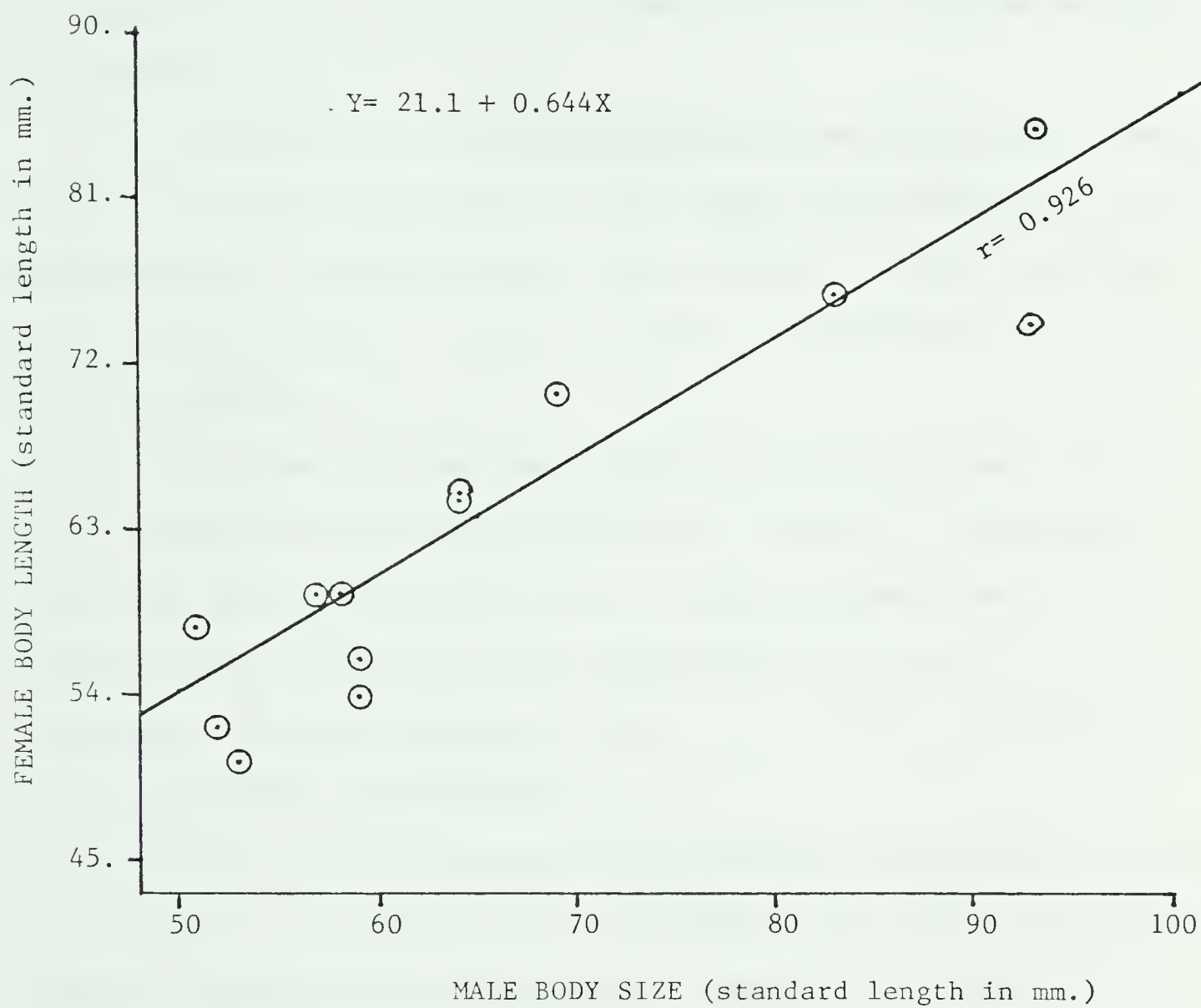
4.3 DISCUSSION

Based on behavioral and ecological observations, it is proposed that both male and female blennies exercise mate choice. This sexual selection process determines the success of a male in attracting females, and the size of the brood they guard.

Huxley (1938) saw two principles acting in sexual selection. He termed behavioral interactions between male and females epigamic selection, and suggested that it favors

FIGURE 4

BODY SIZES OF MALE VS. FEMALE (in mating pairs)



the elaboration of morphological and behavioral features to attract members of the opposite sex.

The second process, intrasexual selection, resulted from behavioral interactions between members of the same sex (usually males). This latter form of selection produces strength and the elaboration of morphological features used as weapons.

An examination of morphological differences within each sex in *O.atlanticus* suggests that such differences are no more elaborate between males than between females and thus, intrasexual selection is not a prime evolutionary force in this population.

Results obtained during this investigation (see section 5.2.2) and those obtained by Marraro (1978) do indicate that there are strong behavioral differences between males and females displayed during the reproductive periods.

Therefore, epigamic selection may very well be the prime selective force acting here.

Trivers (1972) proposed that parental investment is the key factor influencing sexual selection; the sex making the smaller investment in the progeny competes for mates and is subject to sexual selection. Sexual selection based on preference for one sex will lead to the evolution of sexually dimorphic characters in the other.

Sexually dimorphic characters do occur in redlip blennies. Males bear a fleshy, rugose knob on each anal spine while females incorporate and obscure the first anal

spine in a triangular fleshy fold which embodies the genital opening. However, the near absence of sexual dimorphism in *O.atlanticus* points out that both sexes invest in the progeny. There is ample evidence to support this notion.

In some species, particularly in those which both sexes make substantial parental investment, both male and female may exercise mate choice (Halliday 1978). I have already suggested that males and females select their mates on the basis of several features. A feature common to both members is the body size of the mate (Fig. 4). The significance of such pairing is still unknown.

The breeding behavior of many species of tropical fishes is well documented (Keenleyside 1979). There seems to be no general rule by which different species of fishes choose their mates. Also, the literature contains no evidence that mate selection in other species operates in the manner described above.

The habitat of the redlip blenny is a harsh environment. The surge zone is characterized by fluctuations in temperature and salinity, much sediment transport, strong wave action and high predation pressure. To counteract such harshness, both males and females must ensure that the energy they invest in the progeny will not be wasted. They do so by selecting for features which can provide protection against these elements. Weak evidence has been provided to suggest that nest emplacement may be important in this regard. However, other evidence suggests that the main

criteria influencing male and female selection concern body size and nest size. I hypothesize that male body size and nest size may indicate to a female the susceptibility of her eggs to predation and the chances of having all her eggs fertilized. Females therefore select for the largest male possible having an adequate nest. Since female fecundity increases exponentially with length (see section 6.2), males may select the largest females possible to ensure maximum reproductive success. There is thus a conflict between male and female choice since each prefers a mate larger than itself. Observed pairings in the field fall between the two optima.

5. REPRODUCTIVE ACTIVITIES

5.1 DEFINITIONS

Male in reproductive condition: A mature male (greater than 50 mm S.L.) characterized by a high gonadosomatic index, defending a nest.

Breeding period: The period of the month during which a male in reproductive condition will accept females into his nest. This period coincides roughly with the first quarter/full-moon period of the lunar cycle.

Non-breeding period: The period of the month in which a male in reproductive condition will not accept females into his nest. This period corresponds roughly to the last quarter/new moon phase of the lunar cycle.

Nest: A crevice occupied by a resident blenny more often than any other crevice in his territory.

Nesting: A redlip blenny (male or female) is nesting when it remains inside a nest within the boundaries of its territory, for any length of time.

5.2 Reproductive Behavior

5.2.1 Materials and methods

Marraro (1978) monitored the activity budget of male and female redlip blennies during breeding and non-breeding periods. He concluded that males in reproductive condition,

on average, did not spend more time within or next to the nest than males in non-reproductive condition.

However, my preliminary field observations suggested that significant changes in nesting activity were exhibited by redlip blennies during the breeding period. In order to obtain more information on this, 120 time budgets on *O. atlanticus* were done during the 1980-81 field season. These time budgets were taken as follows:

Throughout the lunar cycle, a series of dives were made in the surge zone between 9:30 and 11:30 AM. I would find a redlip blenny at random on the reef, anchor myself to the substrate at a distance of 3 m from the fish and observe its activities. During the first 5 minutes, I would allow the fish to become familiarized with my presence. Then I would record the period of time spent by the fish inside a crevice and outside the crevice. At the end of the observation period, which lasted 10 to 30 minutes, the fish was killed and the nest inspected for the presence of eggs. The size and sex of the fish was determined in the laboratory.

5.2.2 Results

Table 2 reveals that mature females, if not harassed by predators or large fishes, spend no more than 29% of their time nesting during the morning. Throughout the month, the average time spent nesting is 9.5% of the total time available. A closer examination of individual time budgets reveals that under normal circumstances, females never

TABLE 2

FEMALE NESTING ACTIVITY

| LUNAR DAY (+) | NESTING TIME (*) | SAMPLE SIZE | MEAN % | STANDARD ERROR |
|---------------------|------------------------|----------------|-----------|-------------------|
| -16, -14 | 0-7 | 2 | 3.5 | 3.50 |
| -13, -11 | 0-24 | 8 | 8.6 | 3.35 |
| -10, -8 | 1-29 | 5 | 11.0 | 4.89 |
| -7, -5 | 0-25 | 8 | 11.3 | 2.96 |
| -4, -2 | 5-26 | 3 | 18.7 | 6.94 |
| -1, +1 | 0-17 | 6 | 5.3 | 2.54 |
| +2, +4 | 3-25 | 7 | 10.9 | 3.01 |
| +5, +7 | 1-23 | 4 | 10.8 | 5.05 |
| +8, +10 | 0-25 | 8 | 10.5 | 3.89 |
| +11, +13 | 3-19 | 5 | 9.4 | 2.85 |
| +14, +16 | 0-7 | 2 | 3.5 | 3.50 |

(+) Lunar day 0 = full moon

(*) Nesting time is defined as the time spent inside a nest within a period of 10 minutes. The resulting ratio is expressed as a percentage. The figures cited are the ranges in the % observed for that period.

remain inside a crevice more than 60 seconds consecutively, the average being 19.6 seconds.

The frequency distribution of individual observations of female nesting activity (in % total time) is presented in Fig. 5.

Results of a Kolmogorov-Smirnov test for normality revealed that the distribution of nesting times differed significantly from a normal distribution. The data were transformed using the equation:

$$X = \arcsin (\text{nesting time} / \text{total time})$$

A one-way analysis of variance was done using the transformed data. No significant differences were found between mean nesting times exhibited by females throughout the lunar cycle.

Table 3 shows that the range in nesting time exhibited by males, varied considerably throughout the lunar cycle. On average, nesting activity increases from the new moon interval (-15 or +15) until the time interval succeeding the full-moon period (+2, +4), and decreases thereafter.

Results of a Kolmogorov-Smirnov test for normality revealed that both the distribution of individual observations of male nesting times (in Table 5), and the transformed data, differed significantly from normality. Therefore, the data was arbitrarily classified within 5 lunar intervals. This data was analysed using a Kruskal-Wallis test. Significant differences in male nesting times were observed between some monthly intervals. Non-parametric multiple comparisons were

FIGURE 5

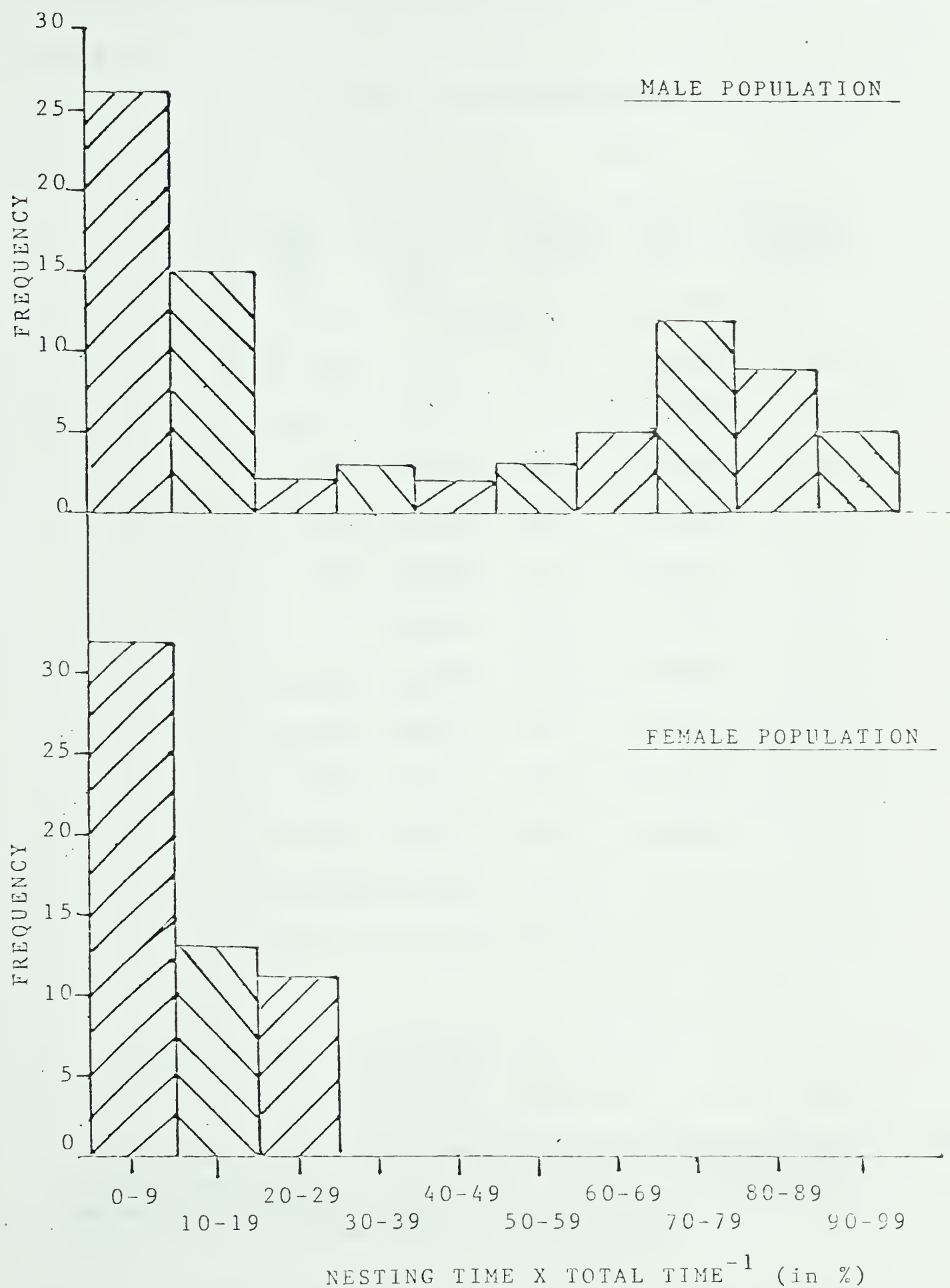
FREQUENCY DISTRIBUTION OF NESTING TIMES IN O. ATLANTICUS

TABLE 3

MALE NESTING ACTIVITY

| LUNAR DAY (+) | NESTING TIME (*) | SAMPLE SIZE | MEAN % | STANDARD ERROR |
|---------------------|------------------------|----------------|-----------|-------------------|
| -16, -14 | 0-11 | 7 | 4.14 | 1.62 |
| -13, -11 | 3-16 | 7 | 9.86 | 1.55 |
| -10, -8 | 0-80 | 10 | 25.80 | 9.86 |
| -7, -5 | 10-88 | 8 | 54.25 | 10.50 |
| -4, -2 | 34-86 | 9 | 65.56 | 5.68 |
| -1, +1 | 35-92 | 8 | 72.89 | 6.03 |
| +2, +4 | 70-94 | 8 | 80.88 | 3.78 |
| +5, +7 | 20-89 | 5 | 56.00 | 13.14 |
| +8, +10 | 0-18 | 6 | 10.83 | 3.39 |
| +11, +13 | 5-10 | 7 | 8.86 | 1.22 |
| +14, +16 | 0-12 | 7 | 4.15 | 2.64 |

(+) Lunar day 0 = full moon

(*) Nesting time is defined as the time spent inside a nest within a period of 10 minutes. The ratio obtained is expressed as a percentage. The figures provided here are the ranges in the % observed for that period.

done on the same data to determine where the differences were located. The results are shown in Table 4.

The results outlined above suggest that males undergo significant change in their nesting behavior throughout the lunar cycle. Although significant changes in male nesting activity occur throughout the lunar cycle (nesting activity increases from the new moon to the full moon and decreases thereafter), the most pronounced change (significant increase in nesting activity) occurs between the first quarter (FM-10 to FM-5) and the full moon (FM-4 to FM+4). This clearly indicates that spawning begins mostly during the week preceding the full moon period, while hatching occurs throughout the period following the full moon (FM 0 to FM+13).

Data on nesting behavior of females and males is jointly presented in Fig. 6. Results of Student t-tests (for samples of unequal variances) revealed that the average male nesting time differs significantly ($P < 0.05$) from that of females for the period ranging from the first quarter of the lunar cycle (FM-7) to the last quarter (FM+7).

The results outlined above are best explained in terms of spawning behavior. As described by Marraro (1978); "generally breeding occurs during the full moon phase of the lunar cycle. Reproductive activities are carried out within the territory of the male. Adhesive eggs are deposited within a nest cave which has been prepared by the male. The eggs are maintained by the male until hatching occurs".

TABLE 4

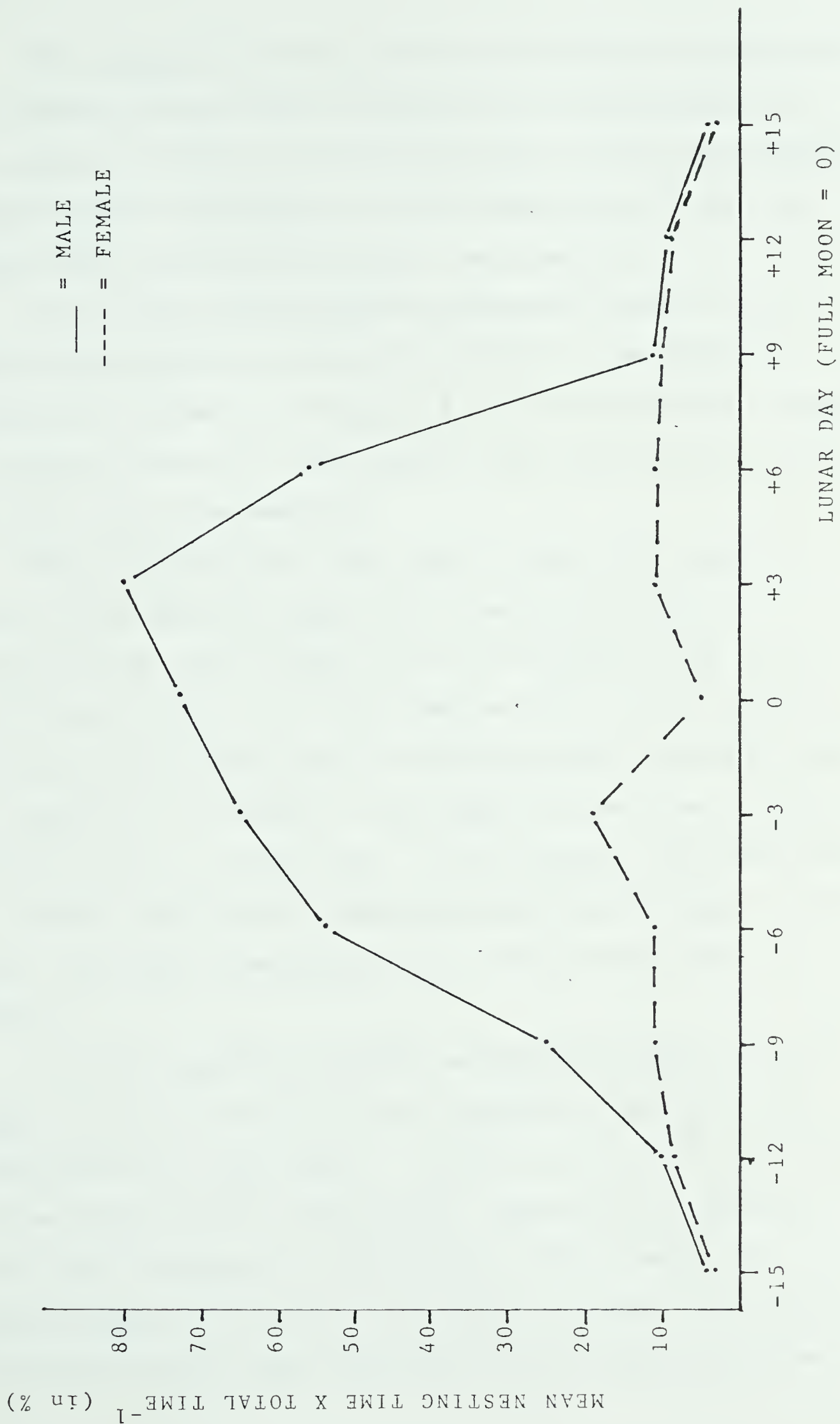
ANALYSIS OF MALE NESTING TIME

| | | | | | |
|-----------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| LUNAR INTERVAL | NEW MOON | | | | |
| NEW MOON -16, -11 | ----- ----- ----- | FIRST QUARTER | | | |
| FIRST QUARTER -10, -5 | | ----- ----- ----- | FULL MOON | | |
| FULL MOON -4, +4 | * | * | ----- ----- ----- | LAST QUARTER | |
| LAST QUARTER +5, +10 | | | | ----- ----- ----- | NEW MOON |
| NEW MOON +11, +16 | | | * | | ----- ----- ----- |

* = Significant changes in nesting times occur between the two periods (Kruskal-Wallis test, $P < .05$)

FIGURE 6

O. ATLANTICUS NESTING BEHAVIOR THROUGH TIME



This suggests that the lunar cycle and the presence of eggs inside the nest may influence male nesting behavior. The separate effects of both factors can be distinguished by comparing the time budgets of males with and without eggs inside their nest during the full moon period.

In all cases where eggs were observed inside a nest, males always spent more than 52% of their time inside it (nesting), the average being 73.4 %. All males without eggs, throughout the entire lunar cycle, never spent more than 50% of their total time nesting.

Males spending more than 52% of their time nesting exhibit nest-guarding behavior. No males involved in nest-guarding remained more than 30 seconds outside their nest without returning inside the nest for a brief period. The average time spent out of the nest before returning was 6.1 seconds. The length of time spent inside a nest before emerging from it ranged from 1 to 80 seconds, the mean being 31 seconds. Nest-guards remained significantly longer inside their nest before emerging from it, than females did in theirs.

The nest-guarding behavior exhibited by males having eggs inside their nests is well documented (Marraro 1978). Nest-guards not only spend a larger proportion of their time inside their nest but show greater aggressivity towards inter and intraspecific individuals, than do males not guarding eggs. This particular behavior played a key role for identification when searching for nest-guarding males.

The data provided above justifies the use of nest-guarding behavior as a good indicator of spawning and hatching periodicity in redlip blennies. By periodically swimming along a transect line positioned over the territories of redlip blennies, an observer can obtain an accurate figure of the number of nests containing eggs merely by counting individuals exhibiting nest-guarding behavior.

5.3 Reproductive Periodicity

Based on information from spawning behavior, Marraro (1978) found a significant correlation between the number of spawning incidents and the full-moon phase of the lunar cycle. He concluded that the ultimate factor responsible for spawning rhythm in redlip blennies was not clear. In this investigation, an alternative approach was used to determine the factors responsible for the spawning pattern.

5.3.1 Materials and Methods

During May 1980, a transect was established in an area occupied by redlip blennies. The study site chosen was situated on the west coast of Barbados about 1 km north of Hometown, at the end of Heron Bay.

An area (57 m X 1.1 m) was permanently marked by attaching or nailing a nylon rope to the reef in the surge zone, at a depth ranging from 0.5 to 2.5 m. Redlip blennies inhabit the

shallow water surge zone at such depth and live over solid substrate consisting of live coral and coralline rock.

During the periods of May-August 1980 and February-September 1981, I would periodically swim slowly above the transect and record the total number of redlip blennies exhibiting nest-guarding behavior.

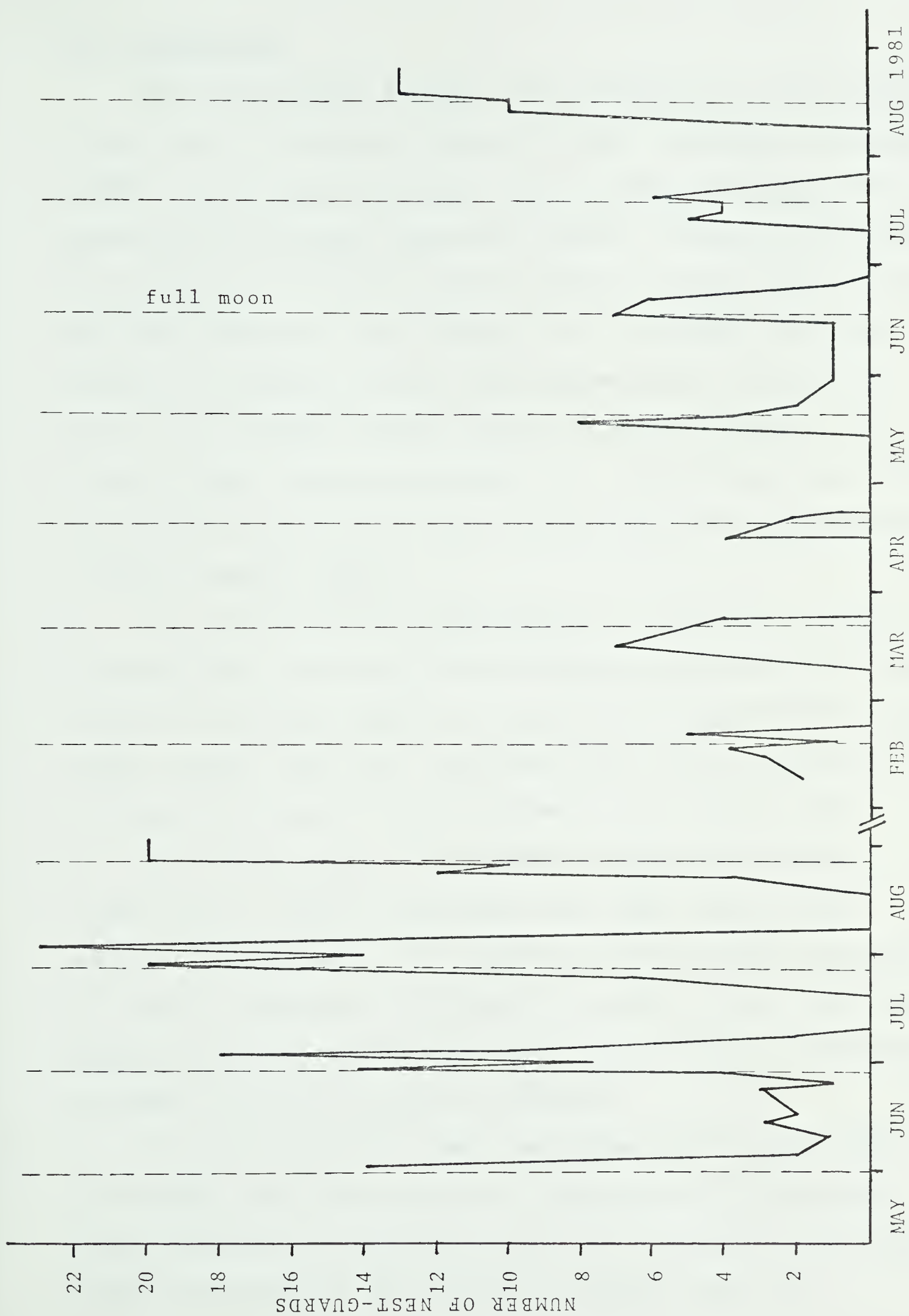
5.3.2 Results

Figure 7 shows the periodicity of nest-guarding behavior of the male population throughout the duration of this investigation. It can be seen that the peak number of nest-guards recorded every month fluctuated during the survey. This is not an indicator of seasonal changes in the reproductive condition of the population, but rather are a function of the total number of individuals in the transect and the maturity of the population (number of juveniles versus adults).

The graph clearly indicates that nest-guarding behavior is correlated with the full moon period of the lunar cycle. The peaks in number of nest-guards do not always occur three days after full moon, as inferred in section 5.2. This suggests that although nest-guarding activity peaks on average, three days after full moon, such periodicity is not constant and may be influenced by some environmental factor. Similar conclusions can also be drawn concerning the periodicity of spawning and hatching.

FIGURE 7

NUMBER OF NEST-GUARDS IN TRANSECT THROUGH TIME



5.4 DISCUSSION

The relationship between the reproductive cycle and the lunar cycle in tropical species is well documented (Johannes 1978). It has been postulated that a common strategy among species having pelagic eggs and oceanic larvae is the timing of spawning to coincide with the ebbing spring tide so as to maximize offshore tidal transport of the larvae. Reduced predation pressures result from deeper water levels that help larvae escape benthic predators such as corals, and from stronger outgoing currents which flush larvae away from reef areas containing a high concentration of planktivorous fishes (Pressley 1980).

During the present investigation, I could not verify if hatching does coincide with the ebbing tide because hatching always occurred at night, during which no observations were made. However the tidal regime was monitored to determine if the period of hatching corresponded to the spring tides.

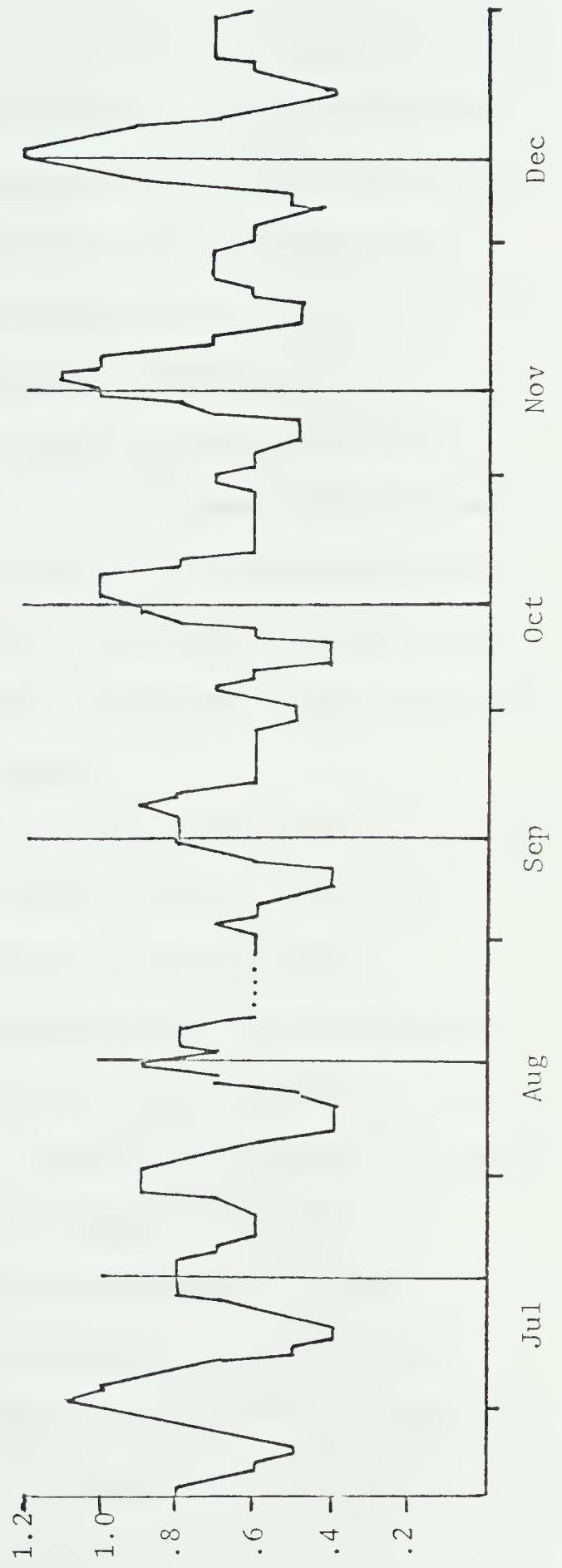
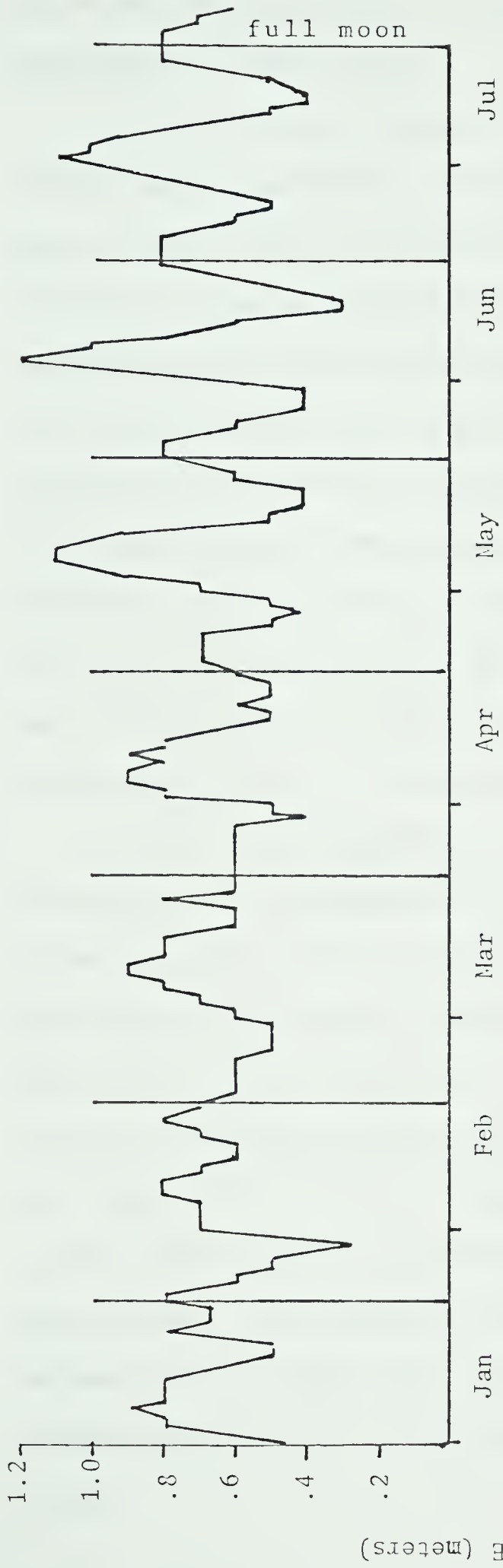
The tidal regime of Barbados is mixed semi-diurnal (Peck 1978). Figure 8 represents the 1981 annual tidal pattern for Barbados. The figures are predictions provided by the U.S. Department of Commerce. Conlon (1973) reported good correlation between them and those of their tide gauge at Bath on the east coast of Barbados.

It can be observed that the highest spring tide does not always occur during the full moon period, indicating that hatching in *O. atlanticus* does not necessarily coincide with the periods of maximum daily change. Thus, no

FIGURE 8

ANNUAL TIDAL REGIME OF BARBADOS (1981)

(vertical lines represent full-moon)



correlation was found to exist between mean hatching time and maximum tidal range.

In fact, Fig. 8 shows that in most cases, the maximum tidal range decreases during the period following the full moon. Thus, hatching generally occurs at a time when the flushing rate decreases in magnitude. This suggests that larvae are flushed away from shallow waters, but not so far as to be carried away from the island. Offshore waters are under the influence of stronger oceanic currents and are characterized by low productivity. All larvae transported to offshore waters would be highly subject to drift mortality. The hatching periodicity observed in *O.atlanticus* may very well be adjusted to ensure the best compromise and therefore maximum survival of the young larvae.

It has been suggested that peak spawning activity among some species of pomacentrids preceeds the full moon by several days so that hatching occurs when nocturnal moonlight is maximum (Pressley 1980). Such an explanation does not fit the timing of spawning in *O.atlanticus*, which results in peak hatching activity during the week following full moon. This is not to say that moonlight plays no significant role in assisting young embryos in their development. But considering the evidence provided, it appears more likely that moonlight is a cue for triggering spawning activity. More research is required to clarify this issue.

Other explanations suggested for lunar spawning cycles include the possibility of greater planktonic food being available during the full moon period, and the establishment of spawning synchrony to swamp predators (Pressley 1980). Since no information was obtained during this investigation on predation pressure and the periodicity of planktonic food, I cannot comment on these issues.

Finally, I believe that there may be more than one explanation to account for the spawning periodicity in redlip blennies and further investigation is required to evaluate the specific effects of each factor mentioned above.

6. REPRODUCTIVE SEASONALITY AND PERIODICITY

6.1 MATERIALS & METHODS

Female gonadal changes were monitored from April to August 1981. Throughout each month (every 4th day), between 6 and 10 female blennies, randomly chosen, were taken for examination. Overall body weight before removal of the gonads, and gonad weight, were measured to the nearest 0.01 g, and standard length to the nearest 0.1 mm. Gonads were preserved in 5% buffered formalin, dissected a few days later. Ova diameters were measured to the nearest 0.01 mm, using a dissecting microscope and micrometer.

6.2 RESULTS

Up to five distinct groups of ova were readily distinguished in each ovary. Asynchronous maturation of several groups of oocytes within an ovary is characteristic of fish species exhibiting iteroparity (Warner, 1975). It has been already established that redlip blennies spawn several times a year (Marraro 1978).

The diameter of the most mature group of ova present in the ovaries ranged from 0.26 to 0.65 mm. Ripe ova were opaque, contained an oil globule, and ranged from 0.56 to 0.65 mm in diameter. These observations agree with those of Marraro (1978).

The spawning pattern of the redlip blenny can be described through the study of oogenesis in females. Figure 9 indicates the size distribution of the most mature group of ova throughout the lunar cycle. These data suggest that spawning, on average, commences 9 days before full moon, and terminates 9 days after full moon.

However, two definite spawning periods can be recognized. There is an initial period of spawning around the first quarter of the lunar cycle (FM-9 to FM-6). The major spawning period commences during the full moon and terminates during the last quarter of the lunar cycle (FM 0 to FM+9). These observations agree with field observations. Further investigation is required to explain the increase in mean ova diameter occurring between the first quarter of the lunar cycle and the full moon.

Gonad weight of females (g) was expressed as a percentage of total body weight (g) to give a gonadosomatic index (GSI):

$$\text{GSI} = \text{gonad weight} / \text{total body weight}$$

The monthly variation in the GSI of females is presented in Fig. 10. Between May and August, 1980, the monthly average in ovary weight ranged from 0.7 to 6.4% of body weight. On average, during each month, 3.4% of the body weight of females goes into the production of eggs. Peters (1981)

FIGURE 9

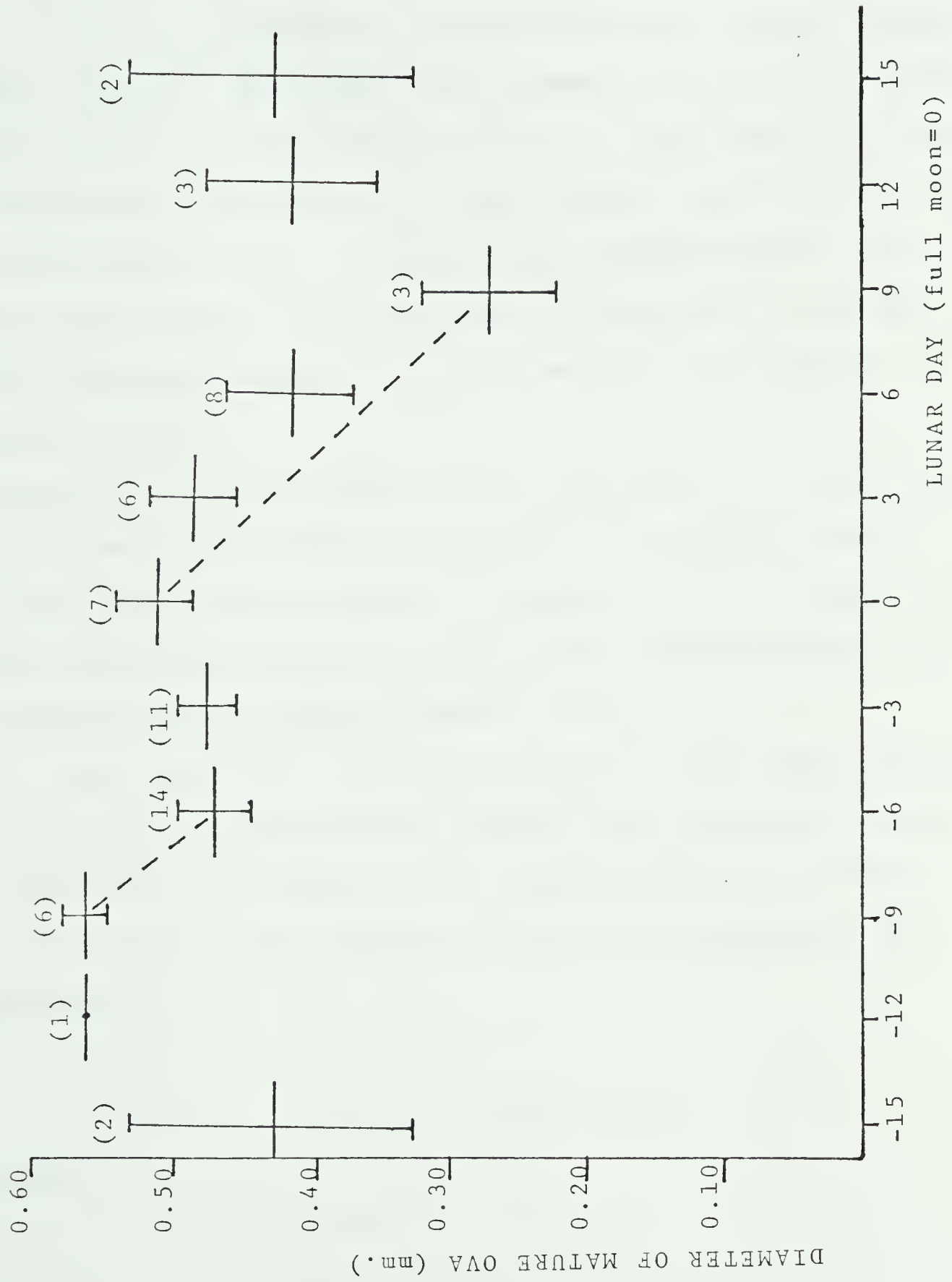
OOGENESIS IN *O.ATLANTICUS* THROUGH TIME

Vertical bar = Standard error

Horizontal bar = Time interval

(number) = Sample size

Dashed line connects points between which significant differences were found (Student t-test, $p < 0.05$).



showed similar trends to operate in the Florida blenny, *Chasmodes saburrae*, where monthly averages throughout the year were shown to range from 0.9 to 8.7% body weight.

To evaluate monthly variation in GSI, the two highest GSI values for each month were summed for better estimates. The results are presented in Fig. 11, and suggest that egg production, per female, is significantly greater during the spring months (April, May) than the summer months (June, July and August). No significant differences in average GSI were observed between the spring months, nor between the summer months.

Fecundity is usually defined as the number of ripened eggs in a female just prior to spawning. In tropical species, since there are no seasonal changes, batches of eggs follow each other continuously and fecundity should account for single batches of eggs (Bagenal, 1978).

Marraro (1978) determined that the total egg production per female of *O. atlanticus* ranged from 1038 to 5900 eggs (mean=3073). He suggested that egg production increases exponentially with length and could be expressed by the equation:

$$F = aL^b \quad (\text{Ricker 1975})$$

where:

F=fecundity

L=total length

a=constant

FIGURE 10

GONADAL STATE OF FEMALE REDLIP BLENNIES THROUGH TIME (1981)

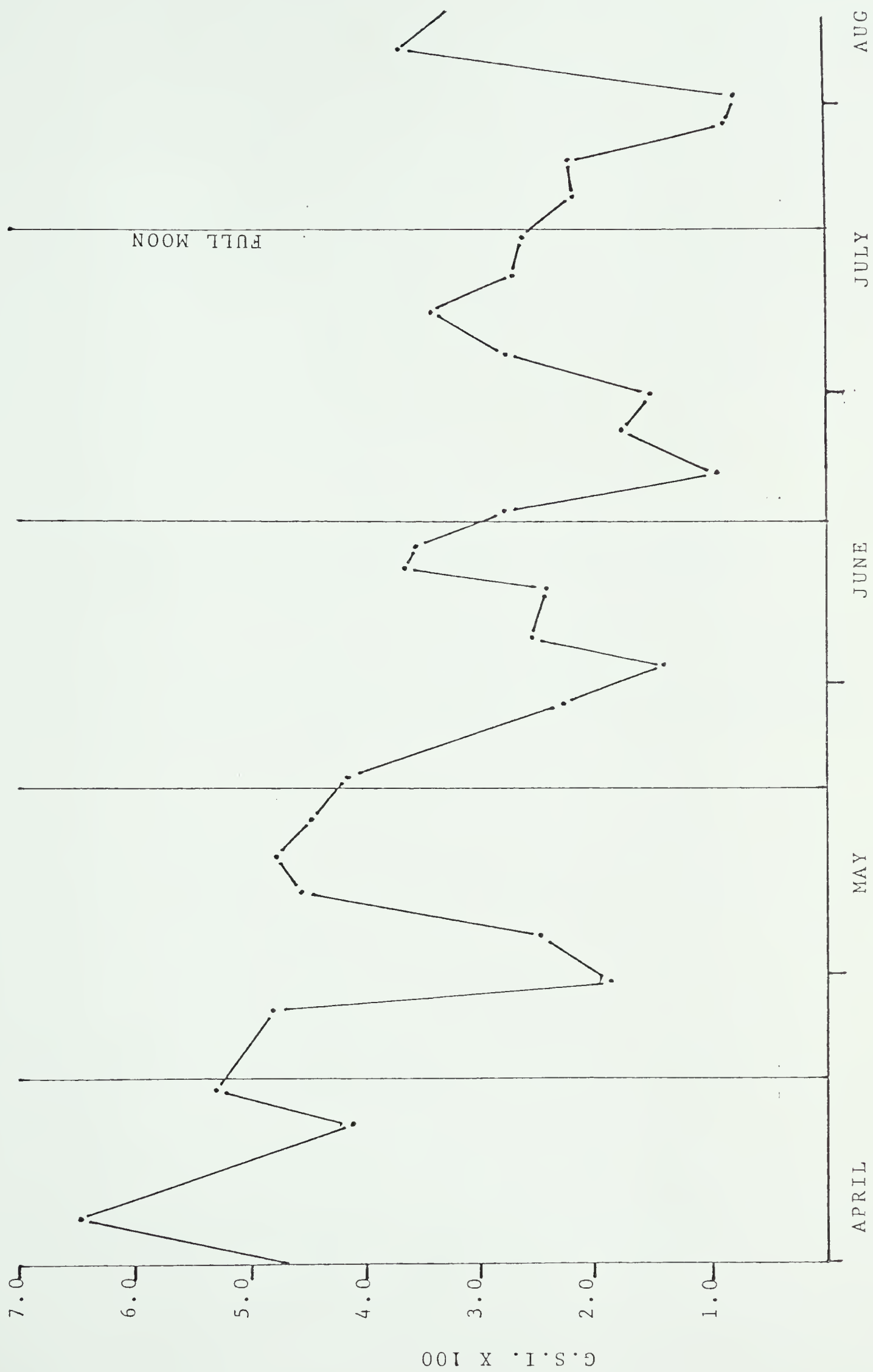
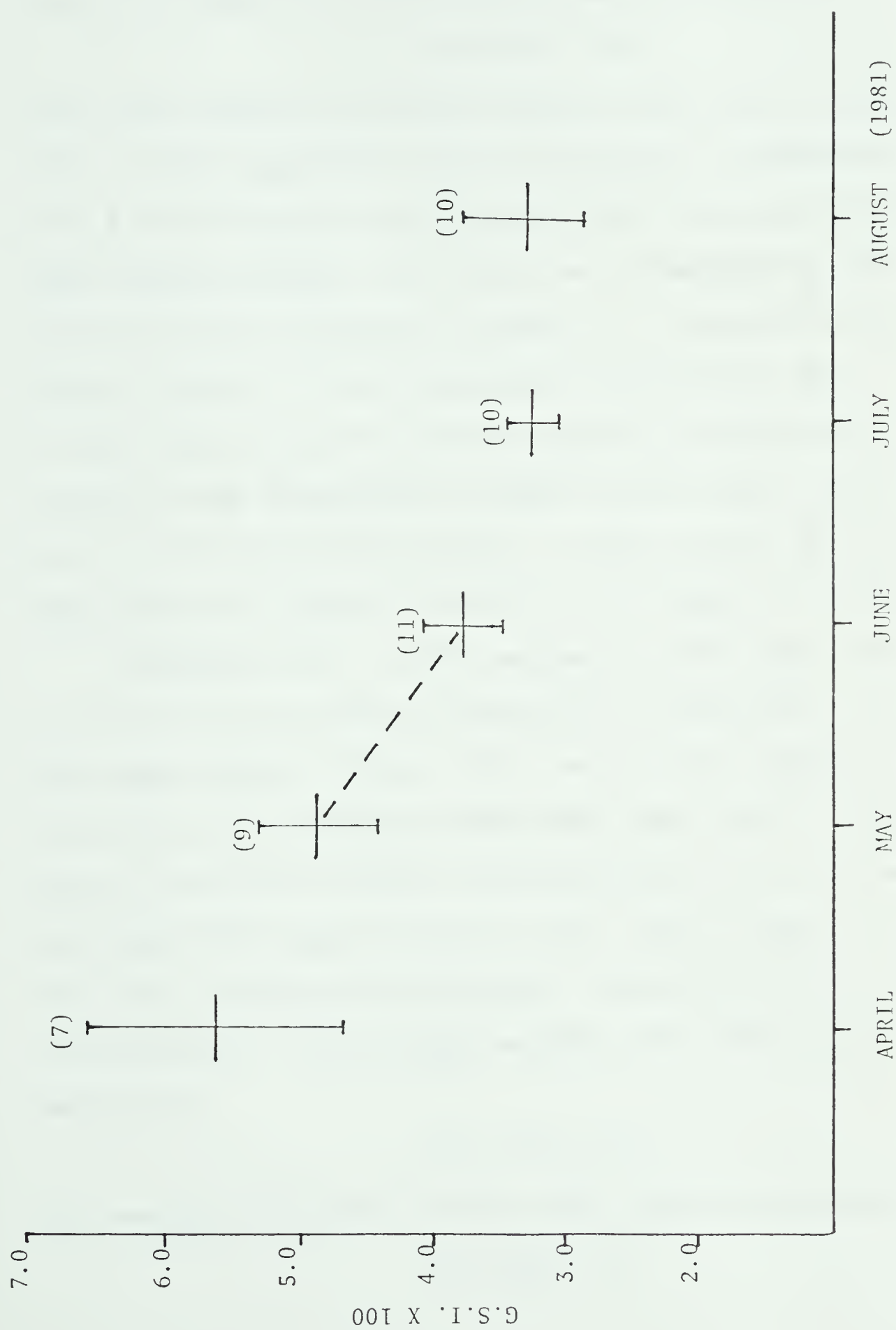


FIGURE 11
SEASONAL GSI OF FEMALE REDLIP BLENNIES (1981)

Vertical bar = Standard error

(number) = Sample size

Dashed line connects points between which significant differences were found (Student t-test, $p < 0.05$).



b=numerical exponent

The relationship for *O.atlanticus* was defined as:

$$F=0.00765 L^{3.449}$$

This relationship was determined by obtaining the dry weight ratio of 200 eggs/whole ovaries. Marrarro recognized that such a relationship could overestimate the actual number of eggs spawned because the latter is influenced by the survival rate of oocytes to maturity. I used an alternative method, similar to that proposed by De Silva (1973), to estimate more accurately the fecundity of *O.atlanticus*. Fecundity was determined through direct visual counts of ova, of the most mature group, in the ovaries of 34 females. Egg production ranged from 794 to 4390 eggs per female.

Stephens et al. (1970) estimated total egg production in the California blenny *Hypsoblennius jenkinsi*, to average 2900 eggs/female. Peters (1981) noted that females of the florida blenny, *Chasmodes saburrae*, when held in the lab during the spring, deposited eggs every one or two weeks and averaged 2600 eggs/fish during that time. Figure 12 shows the 1981 fecundity relationships calculated in the present investigation. The average fecundity for the 1981 April-May period is;

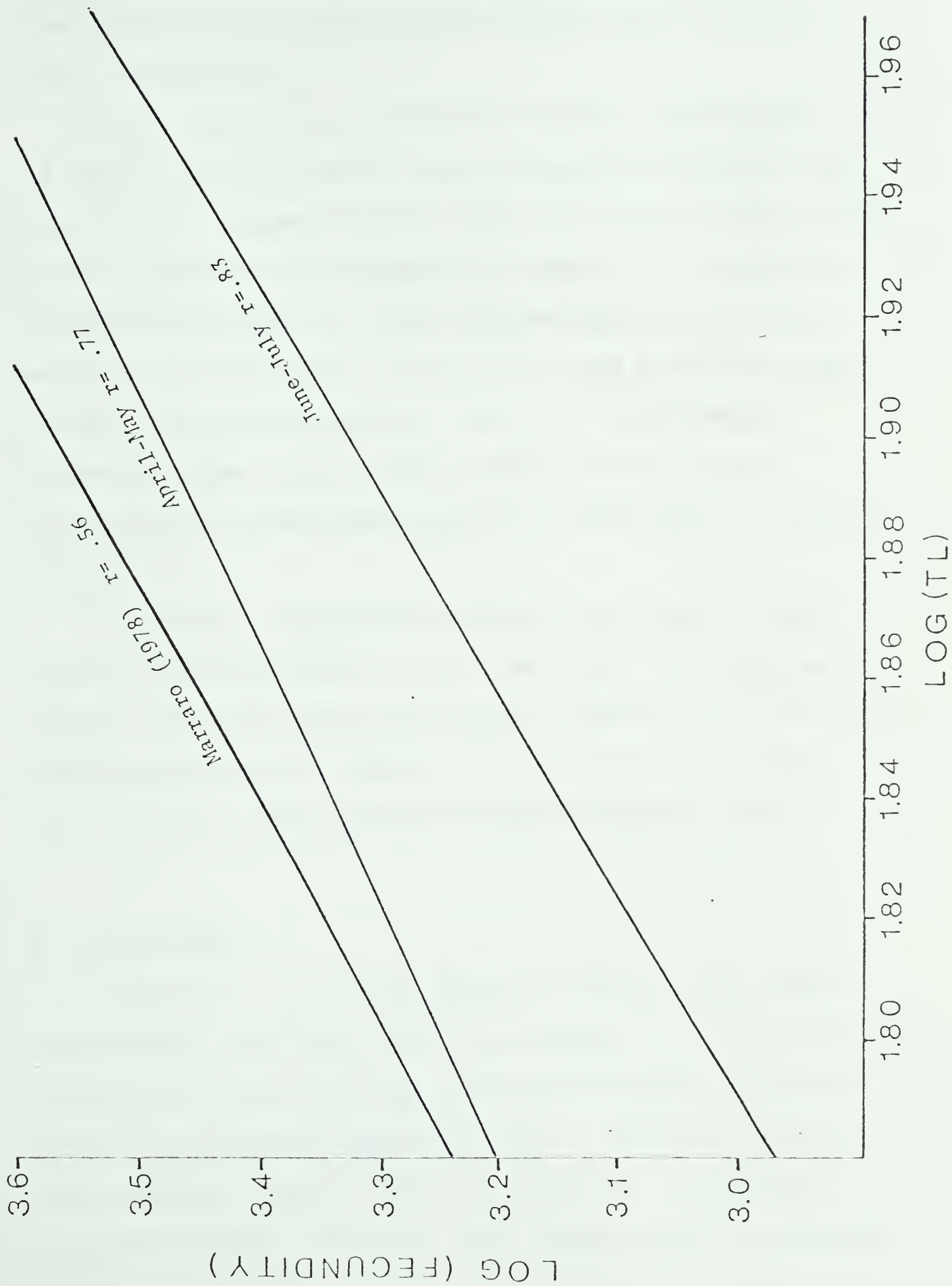
$$F=0.08710 L^{2.39}$$

The average fecundity for the 1981 June-July period is;

$$F=0.00363 L^{3.04}$$

FIGURE 12

SEASONAL FECUNDITY IN *O. ATLANTICUS* (1981)



This evidence indicates that Marraro (1978) overestimated the fecundity of *O.atlanticus* for the April-July period.

Since there is no information on the development rate of ova in redlip blennies, both fecundity estimates were based on the assumption that only ova in the largest group within the ovaries are shed every month. It is possible, although not probable, that ova develop at a rate which permit ova of different sizes to be shed within the same monthly reproductive period. Thus, the relationship suggested above could underestimate potential egg production. Further investigation is required to elucidate this matter.

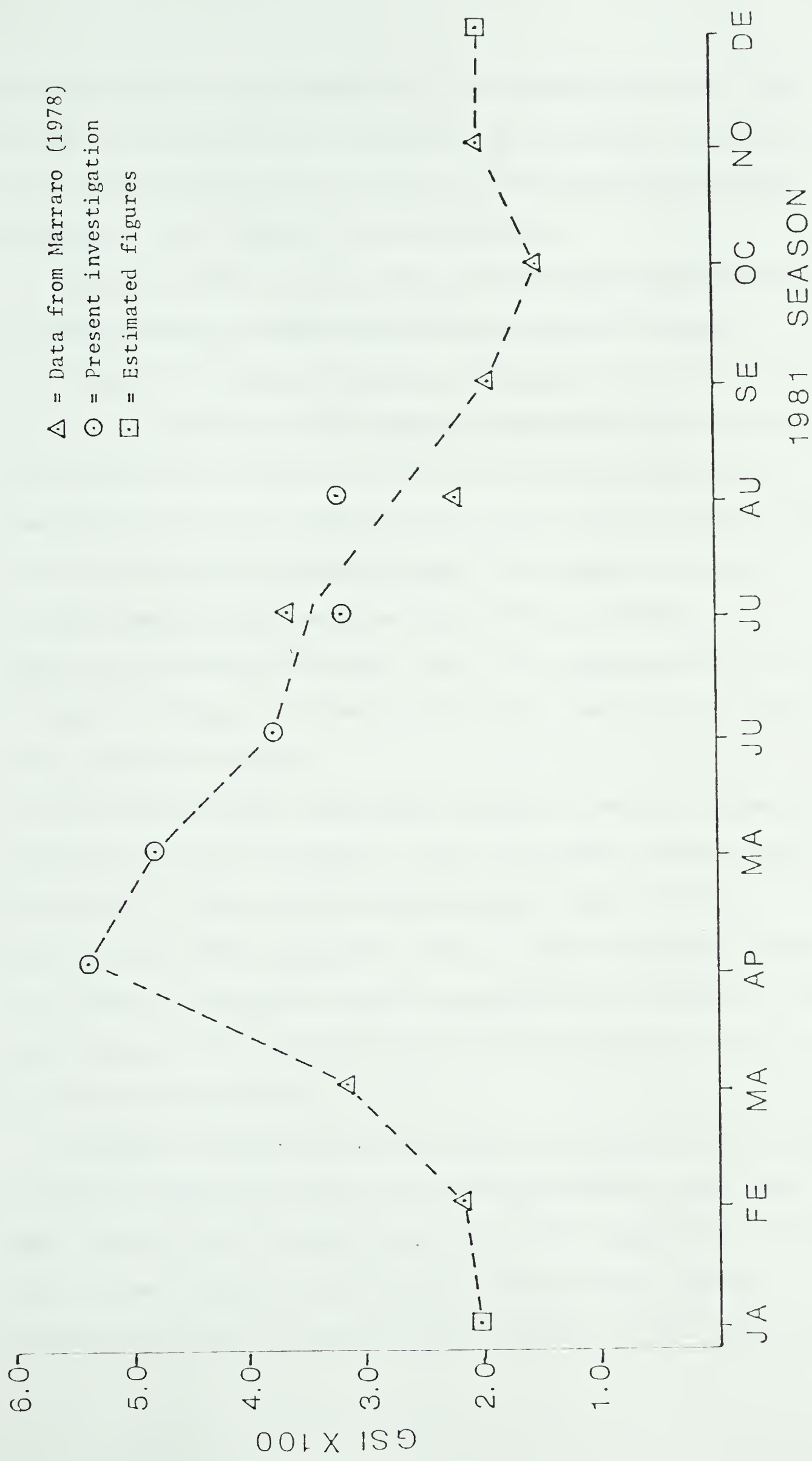
Evidence of degenerating eggs, which had not been spawned, were observed in only one case. This egg mass was large, opaque and appeared somewhat dehydrated. It was also positioned in such a manner as to obstruct the oviduct. I believe that in most cases all mature eggs are shed.

6.3 DISCUSSION

An estimate of annual gonadal change in the female population of *O.atlanticus* is presented in Fig. 13. The data clearly show that peak egg production occurs in spring (April), and lowest egg production in the fall (October). This evidence suggests that the fecundity relationship proposed for April and May, 1981, may be used to estimate

FIGURE 13

ANNUAL FEMALE GONADAL CHANGE (1981)



maximum monthly egg production (per female) for that year. Further investigation is required to formulate a fecundity relationship which will account for minimum monthly egg production (per female) in *O. atlanticus*.

Erdman (1976), in a review of the spawning patterns of Caribbean fishes, found many marine species to spawn year-round, with seasonal peaks occurring once or twice a year, while fewer species showed limited and well defined spawning periods. Munro et al. (1973) investigated the spawning patterns of Jamaican reef fish and determined that there was a general spawning peak from February to April, although members of some families showed evidence of spawning throughout the year. Thus, the spawning pattern of the redlip blenny, is similar, but not identical, to that of other tropical fishes.

It is recognized that spawning seasons of marine fishes are characteristically longer at lower latitudes (Qasim 1955, Munro et al. 1973). Some investigators (Qasim 1955, Harden-Jones 1968) suggested that a longer breeding season for tropical fishes is simply an adaptation to benefit from longer season when temperature and food conditions favor the survival of juveniles.

Johannes (1978) has noted that this explains why long breeding seasons *can* occur but does not explain *why* they occur. Sale (1974), Russell et al. (1974) and Sale & Dybdahl (1975) have proposed that because living space appears randomly on a reef, recolonization is on a "first come, first

served" basis. To increase recruitment under such conditions, a species must spread its reproductive activity over long periods of the year, so as to increase the chances that one of its larvae will be first in line when a suitable territory becomes available (Johannes 1978). Johannes (1978) suggest that year-round feeding in the tropics may mean that, per unit food available, the energetic cost of reproduction, measured as total percentage of total available calories, is comparable with or even lower than those of fishes of higher latitudes.

The spring peak in gonadosomatic index cannot be attributed directly to any biotic factor considered during this investigation and believed to have some effect on spawning patterns of temperate fishes. Steven (1971) found no seasonal variation in the rate of primary production. More & Sander (1977) showed no seasonal variation to occur in either biomass or abundance in zooplankton in waters offshore of Barbados. Sander & Steven (1973) observed no concomitant variation in production rate or standing crop of phytoplankton and zooplankton, and nutrient concentrations around Barbados.

Scott (1961) indicated that in rainbow trout, *Salmo gairdneri*, an insufficient diet caused a reduction in egg number; no data on the diet of *O. atlanticus* is available at the present time which would support or refute this hypothesis.

Finally, Bagenall (1966) reported density dependent factors to operate in Scottish flatfish, *Pleuronectes platessa* L., high densities being correlated with low fecundity. Although the population density of *O.atlanticus* in Barbados did fluctuate extensively (Fig. 21, section 10.2), no correlation was found to exist between the population density of the redlip blenny and its corresponding fecundity value. It should be stated, however, that fairly unusual disturbances (section 10.3) affected the population density of *O.atlanticus* in Barbados during this investigation. A relationship between population density and fecundity may have been masked and further investigation is required to support the existence of such a relationship.

Figure 23 (in appendix) suggests that, in Barbados, the prevailing temperature during April-May ranges from approximately 27.4 to 28.2° C. Year to year differences in fecundity resulting almost certainly from environmental affects are well-established. Rounsefell (1957) correlated sea temperature with fecundity of the pink salmon, *Oncorhynchus gorbuscha*, higher temperatures resulting in low fecundities. Munro et al. (1973) determined that most species studied in Jamaica spawned in spring (February-April), when water temperatures were lowest, but that there was evidence for year round spawning in members of a number of families. Should fecundity in *O.atlanticus* be regulated solely by water temperature, increases in mean GSI values of females should also occur later in the year

(November-December) when water temperatures are within the same range. The absence of such increase in mean GSI for that period, indicates that sea temperature does not directly regulate fecundity. A similar relationship occurs between fecundity and water salinity. I suggest that peak egg production in *O.atlanticus* precedes the summer months when water temperature is highest (above 28.0° C.) and salinity lowest (less than 34.0 ‰). Further investigation is required to determine if such conditions are optimal for the growth of *O.atlanticus* larvae at Barbados. Should this be true, it could be suggested that the reproductive activity in redlip blennies is adjusted to ensure the maximum survival of larvae.

7. REARING EXPERIMENTS

Published information on behavioral and morphological aspects of the early life history stages of *O.atlanticus* (Marraro 1978, Springer 1962) is insufficient to allow for the identification of *O.atlanticus* larvae from the ichthyoplankton.

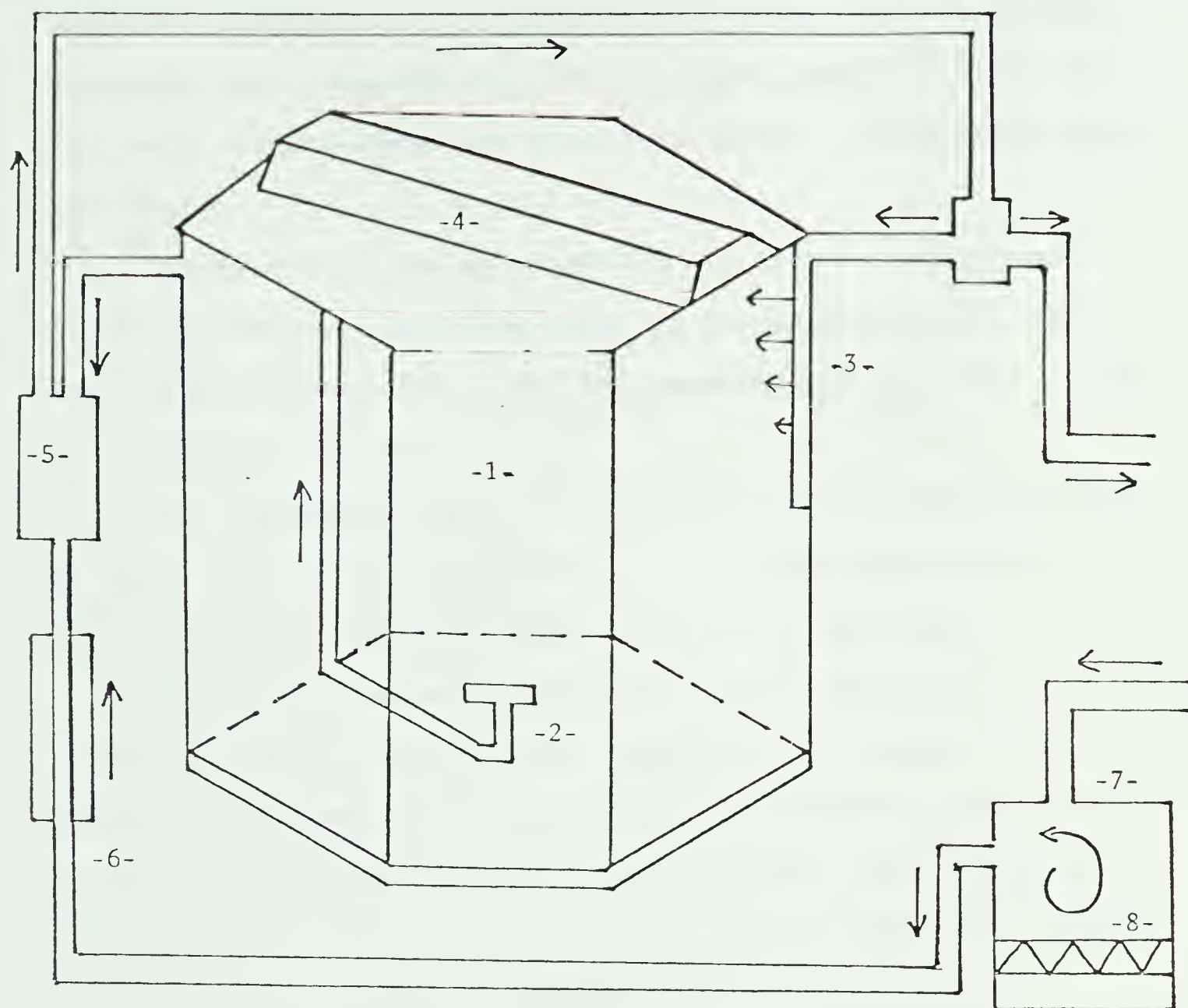
I carried out rearing experiments on the redlip blenny to provide additional information on these stages.

7.1 MATERIALS AND METHODS

An aquarium was built at the University of Alberta and taken to the research lab in Barbados. The design of the aquarium was based on knowledge of Marraro's (1978) rearing experiments with redlip blenny larvae, and of work done by Shackley & King (1978) and Marliave (1976) on the rearing of marine fish larvae.

The aquarium was hexagonal, 1.5 m high, 1.0 m in diameter, and had a capacity of 1800 l. The walls were made of plexiglass sheets (1 cm thick) braced together by four brass belts (3 cm thick X 8 cm wide). All seams were covered with five layers of fiberglass material. Water inside the aquarium was replaced by fresh seawater every day at noon. The complete turnover of water inside the aquarium took approximately 3 hours. Water was first pumped in from the surge zone into a primary settling tank where most sedimentation took place. It was then transferred into a

FIGURE 14: DIAGRAM OF THE AQUARIUM

SPECIFICATIONS:

1. Main aquarium
2. Water outflow
3. Water inflow
4. Fluorescent light source
5. Diatom filter
6. Ultra- violet sterilizer
7. Secondary sedimentation tank
8. Thermo-regulator for water temperature

secondary sedimentation tank to permit the finer material still in suspension to settle out. In this 100 l container, the water was oxygenated with an oxygen pump and air stone. The water temperature was also regulated at this stage when necessary.

A submersible water pump (Little Giant) transferred seawater from the settling tank to the aquarium. The water was irradiated at this point by passing through a U.V. water sterilizer.

The aquarium's water inflow and outflow tube consisted of grey P.V.C. tubing (2.5 cm O.D.). Twenty small holes (1 mm in diameter) were drilled into the inflow tube at 1.5 cm intervals to allow for a gradient in the velocity of incoming current. The outlet opening was situated 14 cm above the bottom. A fine nylon mesh covered its opening to prevent the loss of larvae. Incoming water was slowed to a maximum velocity of 1.5 cm/sec. by passing through a diatom filter which constantly cleaned it.

A fluorescent aquarium light provided the entire wavelength spectrum of daylight. A dim light at night simulated the low intensity light of the full moon. Both light sources were operated manually, to simulate actual daily photoperiod.

The aquarium and the complementary accessories were assembled during May 1980, but were not successfully operated until mid-June 1980. During the following months, redlip blenny eggs were collected throughout the

reproductive period as follows:

Nests of males exhibiting nest-guarding behavior were cracked open using a chisel and a hammer. Pieces of coral to which the eggs were glued, were placed in a large pail underwater and the lid was closed. This container was then brought to the laboratory within 45 minutes. The pieces of coral holding the eggs were deposited on a screen sieve, in the aquarium exposed to a light current of fresh seawater. This procedure was repeated every full moon period during June-Sept/1980 and February-July/1981.

7.2 RESULTS

7.2.1 Embryonic features of *O.atlanticus*

The eggs adhere to the coral substrate by a disc composed of sticky filaments appearing to be an extension of the chorion (Marraro 1978). Newly spawned eggs measured between 0.68 and 0.75 mm in diameter. Redlip blenny eggs are smaller than those of some blennies of temperate latitudes as described by Wourms & Evans (1974), Fishelson (1975), Russell (1976) and Fives (1980). This may be due to the presence of larger yolk reserves in the latter. Furthermore, among members of the Blenniidae, redlip blennies can be described as having a high fecundity; fecundity is normally reported to be inversly related to egg size (Blaxter 1969).

Marraro (1978) observed that newly spawned eggs had yellowish brown yolk, which Fishelson (1976) attributed to the presence of respiratory pigments in the eggs of blennies that spawn in sheltered dark 'nests'. I have observed the yolk in redlip blenny embryos to be pale yellow. Although respiratory pigments may be present, they certainly are not dark in the very young embryos. Darker coloration does develop later (see section 7.2.2) but never appears orange red as in the eggs of *Petroscirtes bhattacharyae* and *Blennius ocellaris* to which Fishelson refers. A general description of the embryonic development in *O.atlanticus* is summarized below. Complementary information from Marraro (1978), has been added to provide a more detailed account of development⁷. Although pictures of all embryonic stages were taken, only the clearest prints are provided in this thesis.

7.2.2 Embryogenesis in *O.atlanticus*

Stage 1: 8 hours after fertilization showing advanced cleavage. The egg membrane is clear and cellular in appearance. The perivitelline space is present. One large oil globule and numerous small ones can be distinguished (plate 1, above).

Stage 2: 24 hours old. Gastrulation has occurred and yolk pigmentation is more pronounced. Epiboly is complete and a well-defined embryonic axis has formed. The anterior

⁷ (*) indicates a quotation from Marraro (1978).

end has expanded into a hemispherical region.

Stage 3: 40 hours old. The optic capsule and lens of each eye are well defined and are partially pigmented. Body chromatophores are apparent as black blotches with irregular outlines. The tail curls around the yolk sac. Somites are present at this stage and the caudal area is separating from the yolk-sac (*).

Stage 4: 50 hours old. Eyes are fully developed and black. The heart is visible near the head and chromatophores appear along the tail.

Stage 5: 58 hours old. The yolk now occupies 1/2 of the egg volume, the heart is functioning and chromatophores are present along the entire length of the tail. One specimen showed 22 somites (*). The auditory sac is visible on each side of the head, the primordial fin is present (*) and the mouth is discernible.

Stage 6: 70 hours old. The yolk now occupies 40% of the egg capsule. Pigmentation of the eye is well developed and silvery due to the accumulation of iridiophores, the pupil appears black.

Stage 7: 90 hours old. The yolk now occupies only 1/3 of the egg capsule. Erythrocytes are present in the blood. Part

PLATE 1: *O. atlanticus* embryos;

8 hours after fertilization (above, magn. 60X)
48 hours old (below, magn. 34X)

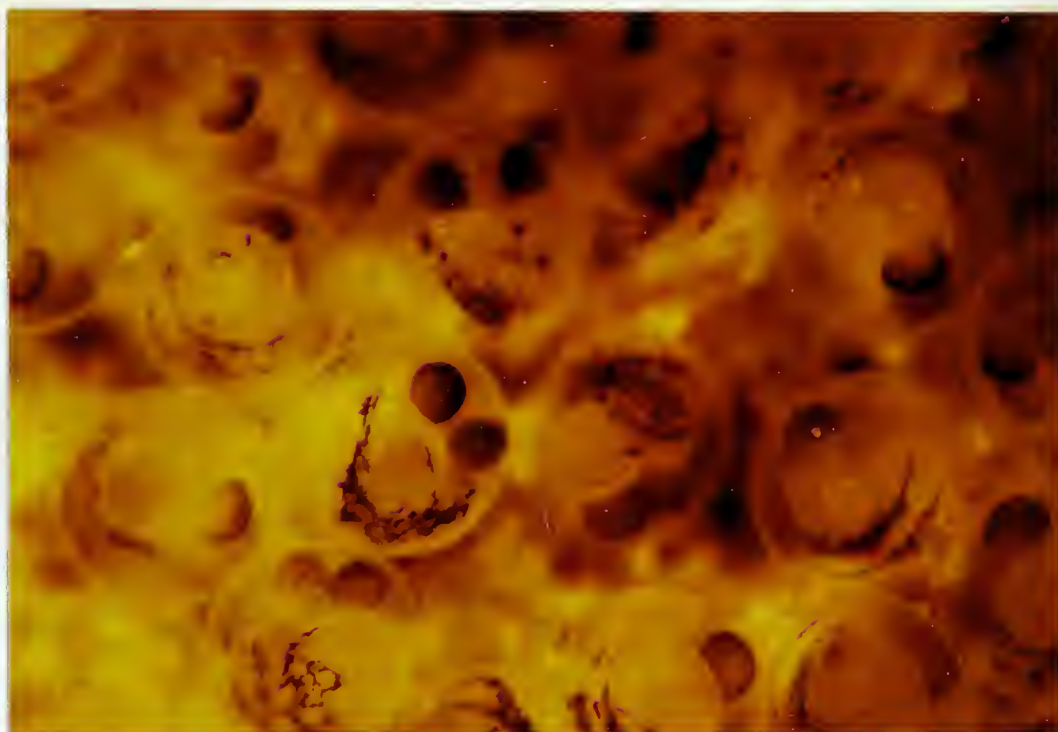
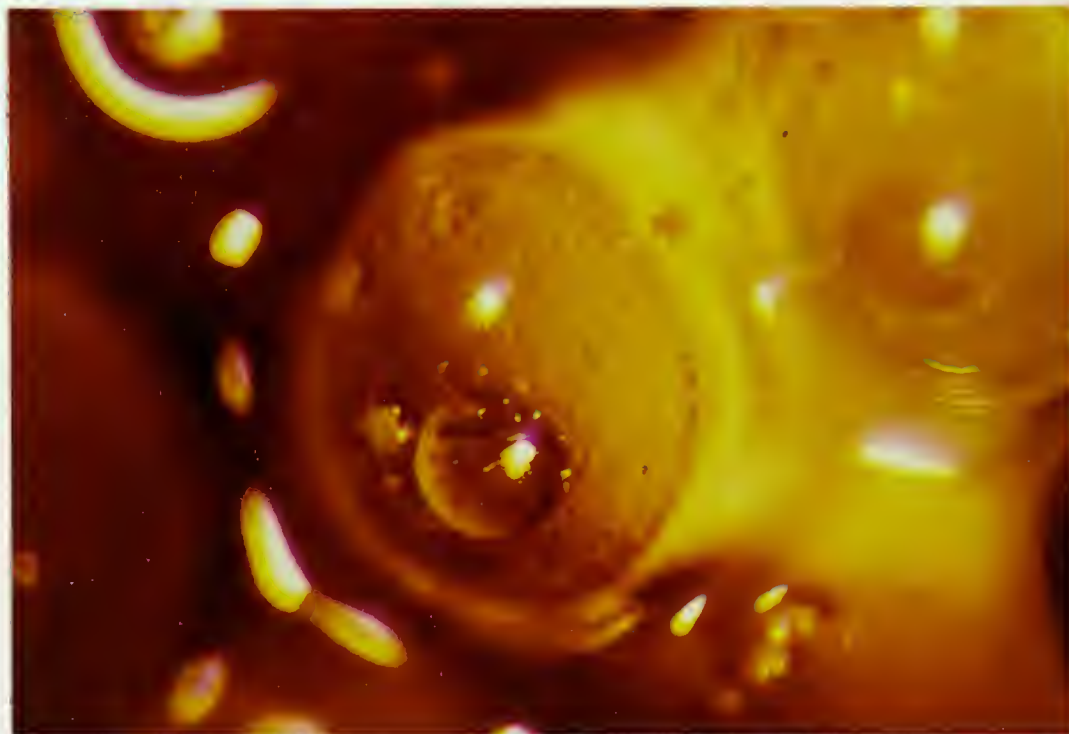
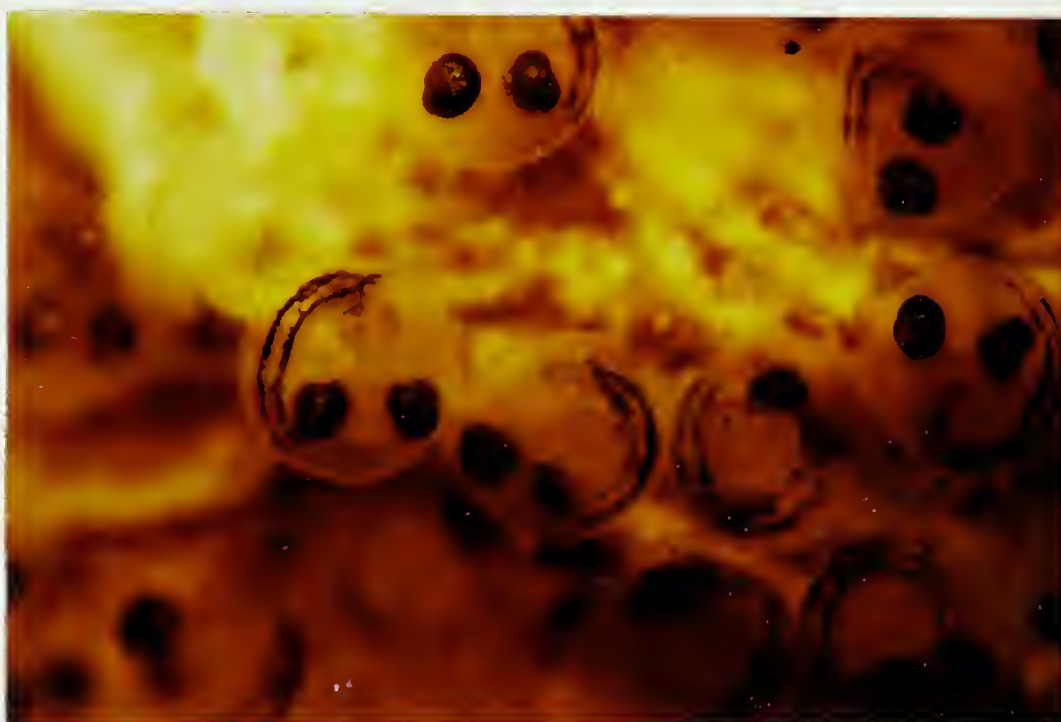


PLATE 2: *O. atlanticus* embryos;

52 hours old (above, magn. 34X)

58 hours old (below, magn. 34X)



of the circulation system containing the erythrocytes, is observable in the pericardial cavity and yolk mass. The head is now large and occupies a position anterior to the yolk mass.

Stage 8: 96 hours old. The melanophores show clearly a 'v' pattern on the ventral side of the embryo, the oil globule is much reduced in size and the embryo is ready to hatch.

7.2.3 Larval morphology (part 1)

Several of my observations suggest that newly hatched *O.atlanticus* larvae are subject to large variations in yolk sac content, number and state of melanophores and length of certain morphological structures. I believe that such variation was probably induced by the following processes:

- A. Differential growth rates brought about by variation in the environmental conditions of the incubating larvae.
- B. Slight changes in environmental conditions prevailing in the aquarium during rearing experiments,

Therefore, the morphological descriptions of larvae which follow are based on cumulative observations of at least 3 larvae of similar developmental stage. All specimens were obtained from the larval population reared in the aquarium. The larvae were killed in MS 222, fixed in buffered formalin (5%) for one month and finally transferred to a solution of 70% ethanol.

PLATE 3: *O. atlanticus* embryos;

74 hours old (above, magn. 34X)

92 hours old (below, magn. 34X)

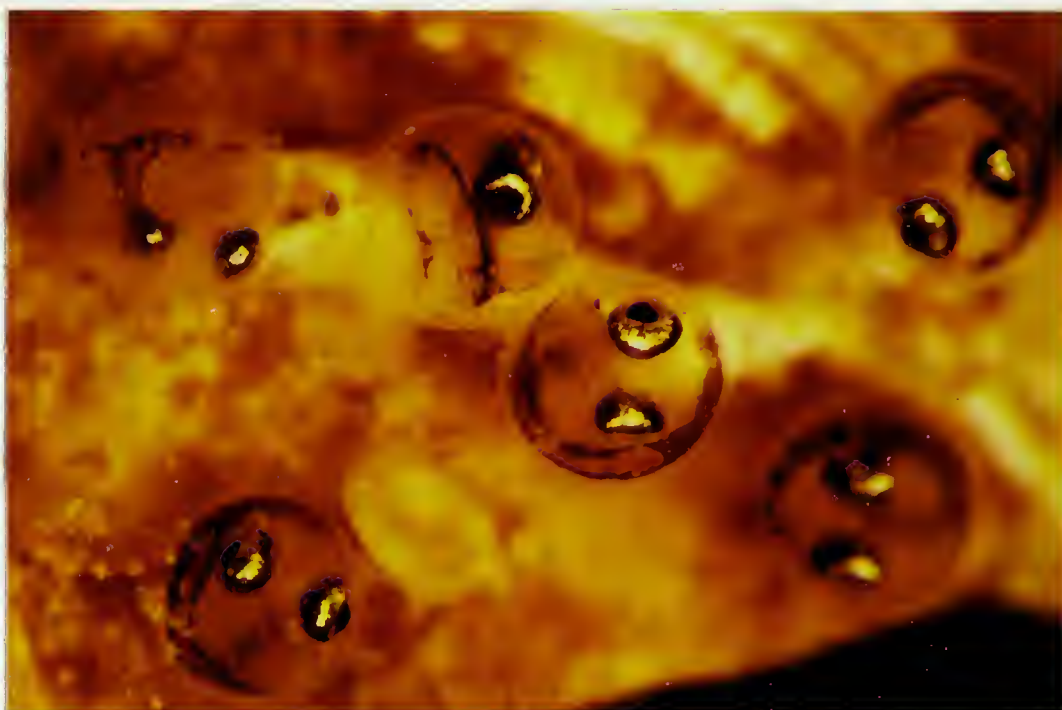
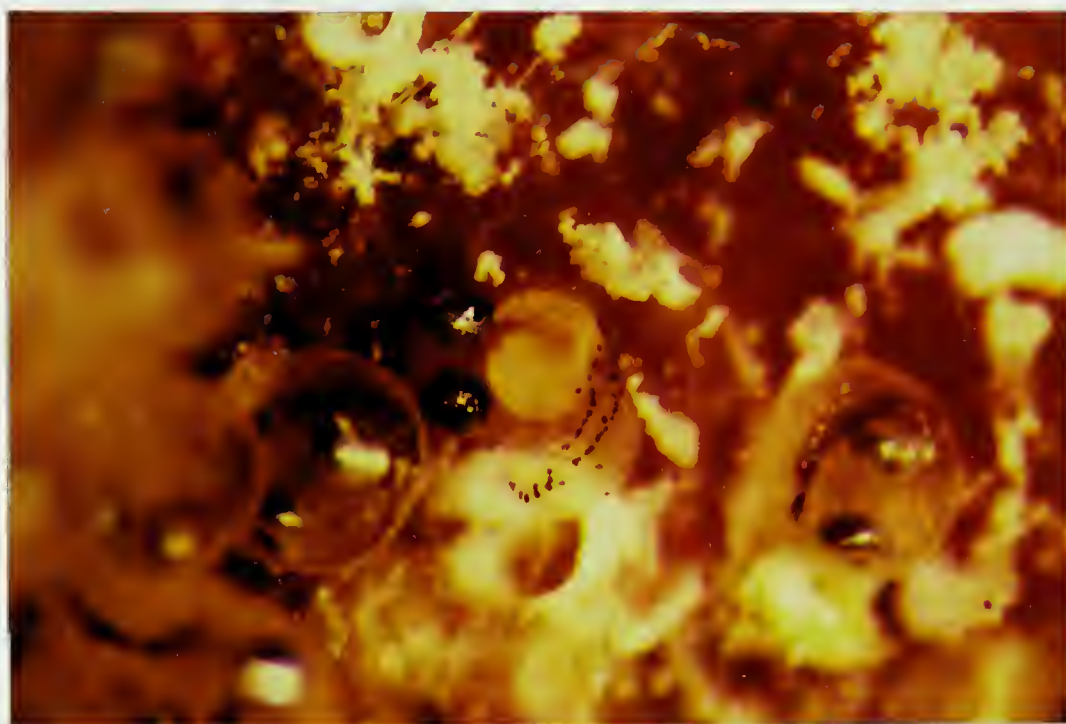


PLATE 4: *O.atlanticus* embryos at hatching
(magn. 34X)



The terminology of anatomical features and development intervals used to describe the larvae follows that of Snyder (1981).

The specimen drawn in Fig. 15 represents a typical 24-hour old larva (late protolarval phase) measuring 2.34 mm (Total length). Three other larvae of the same age ranged from 2.20 to 2.80 mm in length. Marraro (1978) reported a 26-hour old larva to measure 1.80 mm. Marraro also observed that, in his larvae, yolk material represented less than 10 % of the initial yolk volume. I also noticed a marked reduction in the size of the yolk volume but not as large as that reported by Marraro (1978).

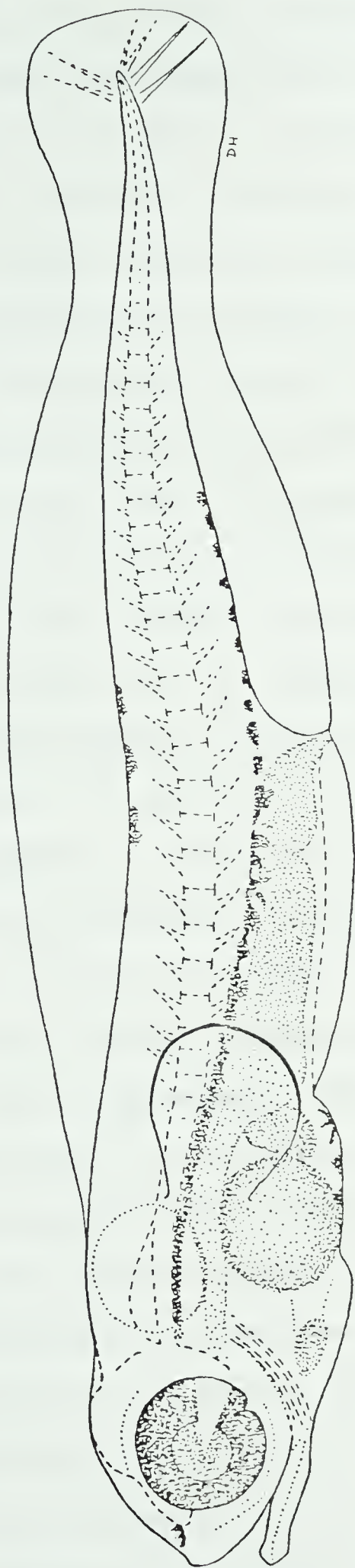
Situated above the yolk sac is a well-developed gut. The foregut appears as a narrow anterior region followed by a wide posterior region and is separated from the hindgut by a sphincter like constriction. The anus is situated at mid-body. The liver lies between the yolk sac and the posterior portion of the foregut and the heart between the yolk sac and the branchiostegal rays, some of which have already differentiated.

Dorsal and ventral processes of the vertebrae are prominent but the urostyle is not yet visible. A few fin rays are beginning to condense in the caudal fin. The primordial marginal fin and pectoral fins are well developed, but fin rays are still lacking. A large otic capsule lies anterodorsal to the pectoral fins on each side of the head. The capsules extend roughly from the insertion

FIGURE 15

DIAGRAM OF *O. ATLANTICUS* LARVA (24 hours old).

(late protolarval phase)



0 .5 1.0
millimeters

point of the pectoral fins to the posterior margin of the eye. The eyes are large and occupy most of the head region, which itself is relatively small. A choroid fissure is present in the lower posterior portion of each eye.

Pigmentation is well-defined in young redlip blenny larvae. A row of melanophores extends from the otic capsule to midway between the anus and the tail region. In most specimens they are punctate or punctostellate, although some are occasionally stellate. Up to ten melanophores are positioned almost longitudinally behind the anus at the base of the ventral fin fold. In older specimens, the number of melanophores in this position is reduced to five or six, and these may occasionally appear stellate. As the row of pigment meets the anus, it splits into two lines to form a 'Y' pattern. Melanophores in each arm of the 'Y' are positioned between the vertebral column and the gut and form two rows above the foregut and hindgut. These melanophores are reticulostellate in newly hatched larvae but tend to become punctostellate in specimens older than 48 hours. Thus, in older specimens, six to eight clearly differentiated melanophores are visible on each side of the gut, between the anus and the origin of the pectoral fin. Occasionally, melanophores may be seen to extend as far the cerebral hemispheres but, as a rule, only one or two cells reach the area behind the otic capsule, above the yolk sac. Between two and four melanophores are also present mid-dorsally at the base of the dorsal fin fold. The

thoracic region underlying the liver and yolk is pigmented by four to six melanophores. These are punctuate but appear reticulate occasionally in some older specimens.

Morphometric data of three well preserved specimens are summerized in Table 5. Since the primary purpose if this description is to permit identification of specimens from field collections, all measurements were made on unstained specimens. The measurements were taken on the left side of the body, by means of an ocular micrometer with a dissecting microscope. All measurements were made along or perpendicular to the body midline. The measurements are defined as follows:

Total length (TL)- symphysis of upper jaw to end of posterior margin of primordial marginal fin or caudal ray (when visible).

Notochord length(NL)- symphysis of upper jaw to tip of notochord (measured in preflexion larvae).

Standard length(SL)- symphysis of upper jaw to posterior edge of hypurals (measured in larvae undergoing notochord flexion and in postflexion larvae).

Eye diameter- horizontal diameter of eye.

Snout length- symphysis of upper jaw to anterior margin of eye.

Head length- symphysis of upper jaw to posterior margin of opercular membrane.

Preanus length- symphysis of upper jaw to anterior margin of anus.

TABLE 5

DESCRIPTION OF *O. ATLANTICUS* LARVAE (24 hour old)

| | (mm.) | (% TL) |
|------------------------------|-------|--------|
| Total length (mean) | 2.78 | 100 |
| Notochord length | 2.66 | 96 |
| Standard length | -- | -- |
| Snout length | 0.14 | 5 |
| Eye diameter | 0.22 | 8 |
| Head length | -- | -- |
| Preanus length | 1.39 | 50 |
| Snout to pect. origin | 0.60 | 22 |
| Pect. fin length | 0.17 | 6 |
| Depth at cleithral symphysis | 0.43 | 16 |
| Snout to pelvic insertion | -- | -- |
| Pelvic fin length | -- | -- |
| Snout to dorsal spine. | -- | -- |
| Snout to dorsal ray | -- | -- |
| Snout to end of dorsal fin | -- | -- |
| Snout to anal fin origin | -- | -- |
| Snout to end of anal fin | -- | -- |
| Depth at caudal peduncle | 0.12 | 4 |
| Caudal fin length | -- | -- |

The measurements provided above do not correspond exactly to those of the specimen drawn of Fig. 15. The values are means based upon the measurements of three specimens.

Snout to pectoral fin origin- symphysis of upper jaw to origin of fleshy lobe of pectoral fin.

Pectoral fin length- length of longest fin ray measured from base to tip.

Depth at cleithral symphysis- vertical distance between dorsal margin of body and ventral symphysis of cleithra.

Snout to pelvic fin insertion- symphysis of upper jaw to anterior margin of pelvic fin.

Pelvic fin length- length of longest pelvic fin ray.

Snout to origin of spinous dorsal fin- symphysis of upper jaw to anterior margin of first developed dorsal spine base.

Snout to origin of soft dorsal fin -symphysis of upper jaw to anterior margin of first developed dorsal ray base.

Snout to dorsal fin termination -symphysis of upper jaw to posterior margin of last developed dorsal ray base.

Snout to anal fin origin- symphysis of upper jaw to anterior margin of first developed anal element base

Snout to anal fin termination- symphysis of upper jaw to posterior margin of last developed anal element base.

Depth at caudal peduncle- least vertical distance between dorsal and ventral margins of body in the area posterior to the terminal dorsal and anal fin rays and anterior to the hypural bones.

Caudal fin length- length of longest caudal fin ray.

It is difficult to determine the degree of resemblance between young *O.atlanticus* larvae and those of other

tropical blenniids since the larvae of very few species have been described at this stage. The only noticeable difference between the larvae of *O.atlanticus* and those of other blenniids concerns the gut morphology. In *O.atlanticus* larvae, the gut is elongate and the anus positioned almost at mid-body, unlike the larvae of *Hypsoblennius sordidus* (Balbontin & Perez, 1979), *Chasmodes saburrae* (Peters 1981), or of temperate blenny larvae such as *Chasmodes bosquianus* (Lippson & Moran 1974), *Hypsoblennius hertz* (Hildebrand & Cable 1938) and *Hiphister atropurpureus* (Wourms & Evans 1974).

More Caribbean blenniid larvae will have to be described before this feature can be recognized as a specific trait, and be used in conjunction with the chromatophore pattern to distinguish redlip blenny larvae from other blenniid larvae.

7.2.4 Behavioral observations of redlip blenny larvae

The incubation period ranged from 94 to 100 hours at 28.0-29.0°C. Hatching always occurred during the evening. The exact time of this varied but it never occurred until some hours after sunset.

During the 1980 rearing experiments, I observed that occasionally a large proportion of the larvae on the rack would remain attached to the egg shell by the tail and mid-body. In Pacific salmonids, agitated swimming in pre-hatching embryos causes the rupture of a head gland and the release of enzymes which dissolve the capsule wall.

Agitation of the larva inside the egg distributes the enzymes within the egg. If the larva is weak and fails to struggle during hatching, the enzymes will not be distributed properly within the capsule and can only dissolve a small portion of the wall. The embryo may protrude its head but the rest of its body remains trapped in the casing, and the embryo dies in this position (Childerhose & Trim 1979).

During succeeding trials, it was noticed that eggs in the early stages of development (younger than 40 hours) at the time of transfer from sea to aquarium, were particularly susceptible to this type of mortality as well as to a cessation of normal development.

It thus appears that young embryos are most sensitive to environmental changes and therefore this period is an important period of mortality during embryogenesis. Mechanical shock and slight changes in temperature, oxygen content, salinity and light intensity can induce stress on incubating eggs during transport from sea to aquarium. Resistance to mechanical shocks or non-optimal temperature and salinity may vary with age (Battle 1944). Eggs of marine fishes seem especially delicate until completing gastrulation, although this has not been systematically tested in any species. Perhaps sensitive morphogenetic processes in the early stages or failure to osmoregulate are the causes (Blaxter 1969).

During the 1981 rearing experiments, only embryos in

advanced stages of development⁸ were brought into the lab. Hatching success in these increased noticeably and the type of mortality described previously decreased substantially. However, even under the best conditions, hatching success was never greater than 40%. Redlip blenny embryos are not very resistant to stress and are susceptible to high mortality at hatching. This fact suggests that nest characteristics are important for the survival of embryos.

Upon hatching in the aquarium, the larvae would ascend immediately to the surface and remain there. Most, if not all, fish larvae rise directly to the surface, usually by means of active swimming and simply not because of the positive buoyancy provided by the yolk sac (Marliave 1977). Newly hatched larvae tend to swim to the surface at various angles. Rice (1964) demonstrated that yolk sac plaice, *Pleuronectes platessa* L., orient to gravity, light being only stimulatory. The early importance of the inner ear in orientation suggests that hovering in contact with the surface film may provide the best baseline for gauging a sense of balance and developing horizontal orientation (Marliave 1977).

Because predation risk under surface illumination levels is high, some selective pressure must favor this ascent. One obvious factor is that larvae are certain to enter the surface current drift if they ascend at hatching; higher productivity of suitable food occurs in the photic

⁸ The criterion used was the presence of silver eyes.

zone and wind-driven surface currents provide for dispersal, one of the presumed advantages of planktonic larval stages (Marliave 1977).

On the morning following hatching, all redlip blenny larvae were distributed within the upper three centimeters of water. A large proportion of these could be seen swimming vigorously to keep their head in contact with the surface film of water. After swimming for about 5 seconds, they would rest up to 10 seconds. During this resting period they would slowly sink, head first, then swim up to the surface again. After two to three hours, these larvae gradually became weaker and sank to the bottom of the tank, where they soon died. Larvae exhibiting this behavior could be observed during the first 3 days after hatching.

Colin (1974) described a similar behavior in the larval of several species of gobies. "Before death, most individuals go through a behavior termed 'top skimming' in which the larvae swim strongly to the surface of the water with the head pointed upward. In groups of larvae where many individuals exhibited this behavior, all usually die within 24 hours". No explanations were provided by Colin to account for such behavior.

Although my aquarium contained no larval food during earlier rearing experiments, I do not believe that this lack of food causes such behavior because 'top skimming' is exhibited by newly hatched larvae. Slight changes in temperature and salinity of aquarium water occurred during my rearing

experiments and may have interfered with normal growth, either during incubation or after hatching, to prevent the development of a normal horizontal swimming posture.

Larvae believed to be in good condition, typically hover just below the surface film. On day 1, these larvae can be seen drifting passively with the current in a horizontal position, occasionally showing short bursts of activity mostly forward. Although the larvae appear to be slightly negatively buoyant, their swimming ability is sufficient to maintain them near the surface. These larvae are referred to as exhibiting 'upper level swimming' which is clearly different than 'top skimming behavior' as described previously. As the larvae grew older, they tended to occupy slightly deeper areas in the water column. Depletion of the reserves appears to reduce buoyancy such that older larvae can only maintain their position by swimming more actively. By day 4, no larvae remained at the surface, most would be scattered in the first meter of water.

From day 1 to day 5, it was observed that larvae would migrate from deeper to shallower areas when the light was turned on (although phototactic response decreased as the larvae grew older). During this same period, the larvae did not appear to select for any area along the artificial light intensity gradient provided. This behavior differs from that of the sponge blenny, *Paraclinus marmoratus*, which switches from positive to negative phototaxis within 24 hours after

hatching (Breder 1941).

By day 2, an escape response has developed in *O. atlanticus* larvae. Upon contact with any object, the larvae immediately swim actively in a spiralling path downward for 5 to 8 cm.

As the larvae became older (up to day 4), the swimming pattern changed from erratic forward darting, to periodical darts in other directions. Not only were such bursts of activity used to regain their vertical position in the water but appeared also to be directed at very small objects. Perhaps such behavior corresponds to the development of feeding activity. Marine fish larvae usually initiate feeding before yolk resorption is complete to support increasing metabolic demands. Since the yolk supply is not extensive at hatching and is nearly depleted by day 4, feeding could start as early as day 2. Darting activity seemed to peak one or two days before larval death. As the darting activity ceased, the larvae became weaker and slowly sank to the bottom, as they appeared unable to maintain their position in the water column. No larvae survived longer than 120 hours.

Marliave (1977) observed yolk sac larvae of the cockscomb prickleback, *A. purpurescens*, to become negatively phototactic if starved, but to remain photopositive if fed from the time of hatching. Since there was decline in phototaxis and gradual decrease of activity in my larvae, starvation was assumed to be the cause of death.

Blaxter and Hempel (1963) noted that starved herring larvae, *Clupea harengus*, kept in aquaria became progressively weaker, gradually reaching a point where they would not show feeding behavior even if food was made available. Since it was unlikely that their larvae would recover after passing this point, these authors referred to it as the 'point of no return'. Values for the point of no return for the herring, *Clupea harengus*, are 5 days after yolk absorption at 12°C., and 9 days after yolk absorption (at 9°C.). Wyatt (1972) found that older plaice larvae, *Pleuronectes platessa* L., would not pass this point even after 25 days without food at 10°C. Although the 'point of no return' concept has since been subject to intensive criticism, it is nevertheless useful as an indicator of the stress tolerance of fish larvae. From this point of view, the figures outlined earlier suggest that redlip blenny larvae are not able to survive a lack of food.

7.2.5 Feeding experiments

At the time of my initial rearing experiments, there was no information in the literature on the nutritional requirements and feeding habits of *O. atlanticus* and very little on those of other blenniids.

The darting behavior of the larvae suggested that they were striking at very small objects. Since the aquarium water was filtered and free of particulate matter, it was

thought that the larvae might be striking at small air bubbles in suspension. Bishai (1960) found supersaturated solutions to be harmful if air bubbles were swallowed by herring larvae, *Clupea harengus* L., sucker larvae, *Cyclopterus lumpus* L., salmon larvae, *Salmo salar* L., sea trout larvae, *Salmo trutta* L., and brown trout larvae, *Salmo trutta f. fario* L. This 'gas disease' could be fatal if the larvae failed to eliminate bubbles from their gut and thus lost the ability to maintain proper buoyancy. Although no air bubbles could be seen in the guts of three specimens observed, a large number of small bubbles were present in the upper 100 cm of surface water. These were caused by an improperly sealed diatom filter, which also dispersed them into the incoming current. Most work on oxygen requirements of marine fish larvae suggests that oxygen is limiting only at very low levels. Therefore, during succeeding trials, efforts were made to reduce the formation of bubbles and to decrease slightly the oxygen content of the incoming current. Since gas bubbles were not entirely eliminated, only a slight decrease in striking activity of the larvae was observed. This phenomenon was believed to be a potential source of mortality.

The first feeding experiments consisted of providing food in the form of tropical fish food. Successful rearing experiments, using this type of food, had been made at the University of West Indies (Ann Hickie, pers comm.). As early as day 1, about 1 cm³ of fish food powder was

sprinkled on the surface film three times a day. After approximately 1 minute, the food particles would start sinking slowly in the water but in no case did the water become murky enough to reduce visibility. During repeated trials, no noticeable increase in darting activity of the larvae occurred when compared to the results of trials which no food was supplied. Liquid baby fish food for newly hatched marine fish was also tried, but similar results were obtained.

In the second feeding experiment, I provided some algae to the larvae. Two strains of microalgae used were provided by Dr. Anderson. A few larvae and much algae were placed in a large 2 l Erlenmeyer container partially immersed in aquarium water. No increase or noticeable decrease in larval survival was observed. In one instance, the gut of one of the larvae appeared to contain some yellowish matter, but there was no indication that this was actually some of the phytoplankton and since the survival rate of the larvae was no better than that of the rest of the population, I assumed that this material might be yolk remaining in the gut.

In the third feeding experiment, I provided the larvae with brine shrimps, *Artemia salina*. These were reared in separate holding tanks. Marliave (1981) suggested that densities averaging 1000 organisms/l should be provided. Therefore, as early as day 1, doses of 350,000 nauplii (about 16 ml of brine shrimp eggs) were transferred daily into the aquarium. The larvae did not appear to be

influenced behaviorally by the presence of the shrimps and there was no noticeable increase or decrease in the survival rate of the larvae. Furthermore no *Artemia* were found in the gut of the larvae.

Ursin (1973) suggested a length ratio of predator/prey for some demersal fishes to be 4.63 to 1.00. Using this as a guide for estimating the size of food suitable for *O. atlanticus* larvae, the length of a prey should be about 0.65 mm. This suggests that *Artemia* were not used as prey by newly hatched blenny larvae because they are slightly too large. This dictated the need to experiment with smaller prey.

Until the 1981 feeding experiments, all feeding experiments were done under sterile conditions. Although many investigators succeed in rearing larval fishes of some species by using organisms from daily plankton hauls, this procedure was not tried in 1980 for fear of contaminating the aquarium. Furthermore, there is evidence that injured planktonic organisms of some species may release chemicals which are toxic to fish larvae (Dr. M. Labarbara, pers. comm.). However in 1981, this procedure was tried as a last resort. Microorganisms were caught over inshore waters every second day with a 450 micron mesh net. Contents of the net were then passed through a 750 micron sieve to take out larger organisms. A portion of the remaining plankton was added to the aquarium four times a day. No increase in feeding activity or survival rate was obtained using this

procedure. Repeated trials using the same procedure but with a smaller size fraction of plankton (210 to 450 microns) led to an increase in feeding activity. Although no larvae lived longer than five days, it appeared that slightly larger proportions of larvae survived until day 3 and 4.

Due to time constraints, and lack of plankton nets with a suitable mesh size (<210 microns), no feeding experiments were done using smaller plankton.

One last attempt was made, using embryos of the variegated urchin, *Lytechinus variegatus*. Several sea urchins were collected and brought to the lab. Eggs and sperms were obtained by injecting the urchins with a .5 molar KCl solution. Eggs were then fertilized, permitted to settle, and periodically rinsed with sterile seawater. After 12 hours, 100 micron long larvae hatch and can live without food for 3 days. Upon hatching these larvae were placed in the aquarium.

The method induced an increase in feeding activity immediately after introduction of the embryos, but the densities soon were diluted to negligible levels as too few urchin embryos were used. It soon became evident that massive efforts would be needed to produce sufficient urchin larvae to generate required prey densities and therefore this procedure was abandoned.

7.3 DISCUSSION

Although tropical oceanic systems are recognized as being a relatively stable environment, the near shore sub-tidal zones are not. The fairly unstable environmental conditions of the surge zone imposes various forms of stress upon the biological community. Although juvenile and adult fishes are adapted to such habitats, changes in environmental conditions may threaten the survival of younger stages. Certain stages of developing eggs are particularly sensitive to the influence of physical and chemical agents (Blaxter 1969). Although, the relatively high fecundity of the redlip blenny and its reproductive pattern are adaptations to optimize on the survival of their progeny, the risk of developmental injuries of embryos should also be reduced. The short incubation time of the embryos is believed to represent such an adaptation.

The larval morphology of *O.atlanticus* resembles that of many other blenniid larvae. Redlip blenny larvae differ from those of other blenniidae of temperate latitudes by having smaller yolk reserves.

Cushing (1976) defined larval drift as the migration of eggs and larvae from spawning grounds to nursery grounds. Since larval drift is more extensive and critical in temperate waters than in tropical waters, the ability to endure starvation and the evolution of a large yolk supply to body size ratio are basic requirements of marine fish larvae of temperate oceans. High planktonic diversity in the

tropics (Raymond 1963), associated with high productivity of tropical coastal ecosystems, provides a wide range of suitable food which should be present in sufficient quantities at all times. Given that *O.atlanticus* larvae possess the behavioral attributes to remain near inshore or coastal waters (see section 8.3), there is no need for the evolution of a large yolk reserve. The higher surface water temperatures of tropical environments (as opposed to those of temperate ones) lead to a rapid exhaustion of yolk supply. This process, coupled with the constant availability of food, allow for the initiation of feeding at a very early stage. Results of my feeding experiments support such assumptions.

The noticeable increase in striking activity obtained during the last feeding experiments suggest that newly hatched larvae require preys in the size range of 50 to 200 microns. Such food preference by young larvae is not uncommon. Newly hatched capelin (*Mallotus villosus*), larvae (less than 5.0 mm T.L.) feed on organisms smaller than 250 microns (Dr. W. Leggett, pers. comm.). Colin (1974) successfully reared larvae of gobies on zooplankton in the 56-200 micron size fraction.

My rearing experiments suggest that the presence of proper food before the end of the yolk absorption stage is of prime importance in the survival of *O.atlanticus* larvae. However, it should not be concluded that this is the only critical stage in its life history . It is generally agreed

that massive mortality occurs throughout the early life in larval fishes. Approximately 99.998% of the larvae of marine fishes die before reaching maturity (Cushing 1976). Since most mortality occurs during the very early stages of larval growth, my failure to rear embryos up to the late larval stages was somewhat anticipated.

8. ICHTHYOPLANKTON SURVEY

At the beginning of this investigation, the information on the pelagic larval stages of *O.atlanticus* was almost non-existent. Only Springer (1962) provided a brief description of some anatomical features of pelagic redlip blenny larvae.

Although results of numerous investigations suggest that blenniid larvae are most abundant in near shore waters (Watson & Leis, 1974), this may not be so for the salariine blennies. Leis and Miller (1976) suggested that Pacific salariine blennies have large, modified, pelagic larvae having their peak abundance in offshore waters. Similar conclusions were drawn by Stephens et al. (1970). However Atlantic salariine blennies, of which *O.atlanticus* is a member, have larvae which may occur in both inshore and offshore waters. Indeed, Marraro (1978) quoted Springer as saying that some larvae of *O.atlanticus* were collected over both deep and in shallow water off the coast of Dominica and the Virgin Islands.

In view of the above facts, an ichthyoplankton survey was designed with the following objectives in mind;

- to obtain more information on the morphology of the larval stages of *O.atlanticus*,
- to obtain some information on the behavior and ecology of the larvae,
- to obtain some information on the distribution of the larvae between hatching and recruitment to clarify the

nature and existence of retention mechanisms operating at Barbados.

8.1 MATERIALS & METHODS

The design of my sampling pattern was largely based upon that of a previous investigation on the distribution and ecology of larval fishes in Barbados (Powles 1975). The sampling regime undertaken was influenced by two points mentioned in his conclusions:

catches of larvae of inshore fishes were high at the 180 meter depth contour line along the west coast and low at stations to the east of the island and offshore to the North and West.

blenniid larvae were usually (three times out of four) more abundant in inshore waters (above the 45 m depth contour line) than in offshore waters.

Plankton tows were therefore carried out over inshore, nearshore and offshore waters on the west coast of Barbados during the 1980-81 field season.

8.1.1 Offshore tows

Originally, a monthly sampling regime was proposed to investigate the offshore distribution of redlip blenny larvae. Offshore plankton tows, using the Institute's vessel 'Martlet' were scheduled for every new-moon period throughout the summer (May-August) of 1980.

Double oblique tows were to be carried out over 100, 200, 300 and 400 m of water at stations offshore from the mid-point (Holetown) and northern tip (Crabhill) of Barbados. Such depth are found respectively at 2, 4, 5 and 6 km from the island although there is some difference between the bathymetric profiles of both regions. However, because the vessel was taken out of service, only a single expedition aboard the Martlett was made (May 14/1980). During this expedition, samples were taken at distances of 1.5, 2.5 and 4 km offshore of Holetown and Crabhill. Positions were determined by using sonar in conjunction with a bathymetric map.

Watson & Leis (1974) observed that blennioid larvae were less abundant in night tows than in daytime tows, which seemed to indicate that larvae underwent a 'reverse vertical migration'. Therefore, during this investigation, all tows were taken between 9:00 AM and 5:00 PM. Samples were collected with a neuston net which I designed. The net, made of Tyrelene, was 3.0 m long with a square mouth of 1.0 m² and a mesh size of 1.10 mm. A series of lead weights totalling 13 kilos were installed at the base of the aluminum frame to maintain a 90° angle of attack. A flowmeter (General Oceanics) was mounted across the mouth opening. This flowmeter was calibrated every second month against the Deep Water Harbour in Bridgetown (length= 536 m). The same flowmeter was used during the nearshore and inshore tows.

The techniques used in this survey are described in the FAO Fisheries Technical Paper no. 175 (Smith & Richardson, 1977). Double oblique tows were done during the offshore expedition. The boat's speed was reduced to 2-3 knots (1.0 to 1.5 m/sec.) and the net lowered slowly. An inclinometer was used to indicate the angle of stray on the towing wire and a meter wheel was used to determine the amount of wire released and the depth of the net. The duration of each tow was roughly 10 minutes although some tows were extended to 20 minutes due to mechanical difficulties with the hydraulic winch.

All plankton tows sampled the water column from the surface to a depth of 40 m. It was later realized that all tows should have been done to a greater depth. Ahlstrom (1959) suggested that the larvae of most shallow-water fishes are confined to the thermally mixed surface layer of the water column and recommends that oblique tows from below the thermocline to the surface be used in assessing total number and distribution of ichthyoplankton. Temperature measurements taken during the offshore tows suggested that the thermocline lay deeper than the maximum depth at which samples were taken.

At each station, water temperature and salinity was recorded up to a depth of 80 m with a salinity temperature bridge probe (Kent EIL Co. model M.C.5). Data on atmospheric conditions were also recorded.

After each tow, the plankton net was washed down from the outside to get all the plankton into the cod end. Then, the cod end was removed and the samples were immediately preserved in a buffered solution of 5% formalin.

8.1.2 Nearshore tows

A series of nearshore tows was initiated on May 24, 1980, and terminated on August 10, 1981. During the 1980 season, at the new moon period of each month, plankton tows were done at three locations along the west coast of Barbados. These stations were situated approximately 1 km offshore of Black Rock, Holetown and Speightstown. At each station, samples were taken during the afternoon, above the offshore slope of the banking reef in 60 m of water.

The net used during the offshore expedition was also used in nearshore tows. An apparatus consisting of a steel tripod, pulley and manual winch was used to lower and raise the net in the water. The whole apparatus was installed aboard a 5 m Boston Whaler powered by a 25 hp outboard engine. Separate plankton hauls were made in surface water (0-10 m), the mid-water zone (20-30 m) and in deep water (40-50 m). The exact position of the boat was determined with a portable sonar and by reference to landmark sightings. When the desired position was reached, the boat's speed was reduced and the bow of the boat directed into the current, which normally runs parallel to shore. The net was lowered to a predetermined depth and the speed of the boat

increased to 2-3 knots. The total duration of each tow was 10 minutes. After this period, the engine was stopped and the net brought to the surface by using the manual winch. After each tow, the surface water salinity and temperature were recorded with the probe. All samples were processed as outlined previously.

During the 1981 season, owing to time constraints, only a single monthly tow was done at the Holetown station. Ichthyoplankton samples were collected as outlined previously except that separate tows to specific depths were not done. Instead step-oblique tows were made by pulling the net for 2 minutes at depths of 2, 4, 6, 8 and 10 m successively without stopping. At the end of this 10-minute tow, the net was winched to the surface and the samples processed as outlined previously.

8.1.3 Additional sampling

During August 1980, three plankton hauls were made in surface waters over the offshore slope of the fringing reef approximately 0.5 km from shore. This area is recognized as being part of the inshore waters. These tows were done to determine if larval fishes were more abundant closer to shore. Furthermore, during July 1981, an additional 10-minute tow was carried out every week at the the Holetown station with a sampling regime identical to that described for other 1981 tows. The purpose of these tows was to obtain weekly samples for that one month, to determine if any larval 'pulse'

occurred before or after the new moon phase. Finally, a night tow was conducted during the new moon period of July 1981, in surface waters (0-10 m) at the Holetown station. This 10 minute plankton haul was carried out over the standard course used during daytime tows.

8.1.4 Processing & Identification

Details of the ichthyoplankton survey are presented in table 6. All samples collected were brought back to the University of Alberta. Larval fishes were removed from the plankton under a binocular microscope and transferred to a solution of 70% ethanol. Approximately 6000 larvae were examined, ranging mostly from 3.3 mm to 11.9 mm in total length (excluding Leptocephali). Representatives of different types of larvae were subsequently examined under a dissecting microscope for body proportions and described using characters such as numbers of spines, pigment patterns and myomere numbers.

Before any of the above samples were processed for the presence of blennioid larvae, several *O. atlanticus* larvae collected by Marraro (1978) in plankton tows, were carefully examined. Most larvae he obtained were at a stage of development similar to that described in the previous chapter. This is to be expected, since Marraro towed his net in near-shore waters during the full moon period. However, a few of his specimens were slightly more advanced in development than any larvae I reared in aquarium. The

TABLE 6

ICHTHYOPLANKTON SURVEY DATA

| LOCATION | DATE | F.M. | TIME | DEPTH | VOLUME | TEMP. | SAL. |
|----------|---------|------|-------|-------|--------|-------|------|
| HOLE. | 14/5/80 | +14 | 12:20 | 40 | 661 | 27.7 | 35.3 |
| (200m) | | | 1:00 | 40 | 520 | 27.6 | 35.3 |
| (300m) | | | 1:20 | 40 | 525 | -- | -- |
| SPEIGHT. | 14/5/80 | +14 | 3:45 | 40 | 425 | 27.8 | 35.2 |
| (200m) | | | 4:00 | 40 | 389 | 27.9 | 35.3 |
| (300m) | | | 5:00 | 40 | 362 | 27.7 | 35.4 |
| HOLE. | 24/5/80 | +24 | 5:30 | 25 | 539 | 28.0 | 35.6 |
| | | | 5:10 | 30 | 572 | 27.2 | 36.2 |
| BLACK. | 30/5/80 | +1 | 12:30 | 30 | 580 | 28.0 | 34.5 |
| | | | 12:00 | 43 | 580 | 27.8 | 35.1 |
| SPEIGHT. | 30/5/80 | +1 | 3:30 | 33 | 700 | 28.0 | 34.5 |
| | | | 2:45 | 45 | 722 | 27.9 | 35.0 |
| HOLE. | 18/6/80 | +20 | 3:30 | 7 | 667 | 28.0 | 33.5 |
| | | | 4:00 | 18 | 582 | 27.9 | 33.6 |
| | | | 4:30 | 35 | 555 | 27.9 | 33.6 |
| SPEIGHT. | 19/6/80 | +21 | 3:15 | 10 | 640 | 27.9 | 33.3 |
| | | | 3:40 | 20 | 650 | 27.9 | 33.4 |
| | | | 4:00 | 35 | 696 | 27.9 | 33.5 |
| BLACK. | 20/6/80 | +22 | 2:45 | 10 | 512 | 28.2 | 33.8 |
| | | | 3:15 | 20 | 638 | -- | -- |
| | | | 3:50 | 35 | 656 | -- | -- |
| HOLE. | 17/7/80 | +19 | 4:06 | 10 | 528 | 28.2 | 34.4 |
| | | | 4:35 | 25 | 503 | 28.2 | 34.7 |
| | | | 5:00 | 40 | 538 | 27.7 | 35.4 |
| BLACK. | 18/7/80 | +20 | 3:50 | 10 | 506 | 28.3 | 34.4 |
| | | | 4:15 | 25 | 452 | 28.1 | 34.4 |
| | | | 4:50 | 45 | 545 | 27.3 | 35.7 |
| SPEIGHT. | 19/7/80 | +21 | 6:00 | 7 | 483 | 28.4 | 33.9 |
| | | | 5:20 | 24 | 526 | 28.1 | 34.4 |
| | | | 4:20 | 45 | 571 | 27.0 | 35.8 |
| BLACK. | 14/8/80 | +18 | 5:10 | 8 (I) | 512 | -- | -- |
| | | | 4:35 | 10 | 529 | 28.3 | 33.3 |
| | | | 4:10 | 25 | 602 | 28.1 | 33.6 |
| | | | 3:30 | 45 | 615 | 27.3 | 35.4 |

| LOCATION | DATE | F.M. | TIME | DEPTH | VOLUME | TEMP. | SAL. |
|----------|---------|------|----------|-------|--------|-------|------|
| HOLE. | 15/8/80 | +19 | 5:30 | 8 (I) | 361 | -- | -- |
| | | | 5:15 | 10 | 443 | 28.4 | 33.5 |
| | | | 4:40 | 25 | 481 | 28.0 | 34.0 |
| SPEIGHT. | 16/8/80 | +20 | 5:00 | 8 (I) | 399 | -- | -- |
| | | | 4:15 | 10 | 436 | 28.5 | 33.4 |
| | | | 3:45 | 25 | 472 | 28.5 | 33.4 |
| | | | 3:10 | 45 | 550 | 27.7 | 34.5 |
| HOLE. | 4/2/81 | +15 | 3:00 | 10 | 323 | 27.0 | 35.7 |
| HOLE. | 9/3/81 | +19 | 3:00 | 10 | 375 | 27.5 | 35.5 |
| HOLE. | 3/4/81 | +14 | 3:20 | 10 | 444 | 27.6 | 35.5 |
| HOLE. | 4/5/81 | +15 | 3:30 | 10 | 400 | 27.5 | 35.5 |
| HOLE. | 1/6/81 | +13 | 12:00 | 10 | 469 | 28.0 | 35.0 |
| HOLE. | 1/7/81 | +14 | 2:30 | 10 | 447 | 28.3 | 33.5 |
| HOLE. | 1/7/81 | +14 | 9:00 (N) | 5 | 479 | 28.3 | 33.5 |
| HOLE. | 9/7/81 | +22 | 3:00 | 10 | 410 | 28.1 | 34.7 |
| HOLE. | 21/7/81 | +4 | 3:20 | 10 | 400 | 28.4 | 34.6 |
| HOLE. | 28/7/81 | +11 | 3:19 | 15 | 337 | -- | -- |
| HOLE. | 3/8/81 | +17 | 2:40 | 15 | 389 | 28.6 | -- |
| HOLE. | 10/8/81 | +24 | 4:30 | 15 | 395 | 29.1 | -- |

DEFINITIONS

BLACK. = Black Rock
 HOLE. = Holetown
 SPEIGHT. = Speightstown
 DEPTH = Maximum depth sampled by the net (in meters)
 VOLUME = Total volume of water filtered (in cubic meters)
 TEMP. = Water temperature at that depth (in °C.)
 SAL. = Water salinity at that depth (in parts/thousand)
 F.M. = Number of days elapsed since previous full moon
 I = Inner Channel
 N = Night Tow

exact size of these older larvae could not be determined accurately, because some specimens were damaged and the exact preservation method was unknown. These preserved specimens measured approximately 3.0 mm (TL).

By and large, Marraro's older larvae were similar to the reared ones. A slight decrease in the size of the hindgut was noticed, as well as some coiling in the foregut. The chromatophore pattern appeared identical to that of younger larvae described previously. The most noticeable feature was the presence of four tusk-like canines in the upper jaw and two in the lower jaw. Although larger *O.atlanticus* larvae possess canines in upper and lower jaws (see section 8.2.1), the presence of such canines at this early stage of development was not expected. This characteristic played a key role in the identification of *O.atlanticus* larvae from the ichthyoplankton samples. The final identification of *O.atlanticus* larvae from the ichthyoplankton was assisted by reference to the meristic, morphometric and melanistic patterns of:

- I. Newly hatched larvae reared in aquarium.
- II. Young planktonic larvae captured by Marraro (1978)
- III. Other Atlantic blennioid larvae reported in the literature
- IV. Newly recruited *O.atlanticus* post-larvae

Finally, a list of other blenniids found at Barbados was provided by Dr. A.R. Emery of the Royal Ontario Museum (Toronto, Canada). Knowledge of their habitat, relative

abundance and adult morphology allowed me to consider the range of possibilities among the blenniid larvae examined. Therefore, my final identification of redlip blenny larvae was in part a process of elimination.

Immediately after identification, redlip blenny larvae were separated from other larvae. All samples are stored at the University of Alberta.

8.2 RESULTS

8.2.1 Larval Morphology (part II)

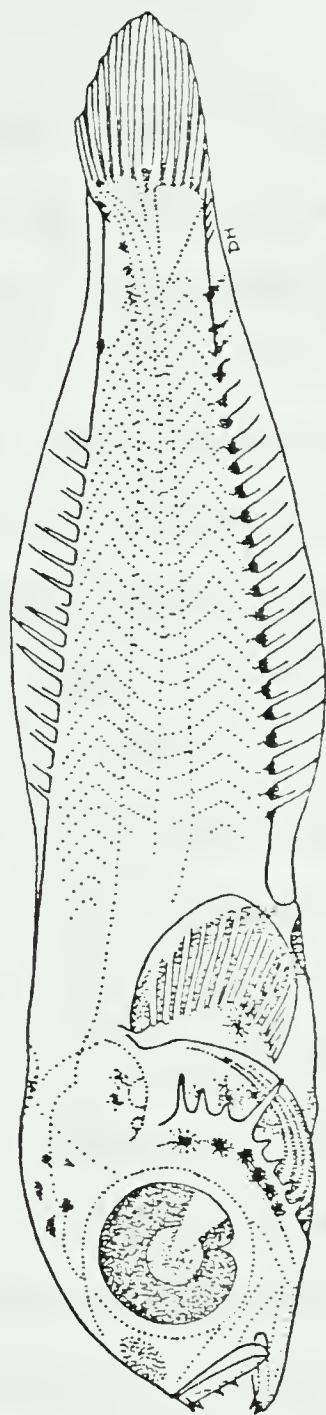
Figure 16 represents one of the most advanced larva of *O. atlanticus* found in the ichthyoplankton samples. Several morphological changes from the younger individuals described (see section 7.2.3, Fig. 15) are obvious at this stage. The entire gut is coiled and the anus is positioned closer to the head. The peritoneum is heavily pigmented on the dorsal and lateral walls of the coelom. The ventral wall is clear except for the presence of melanophores on the anterior tip of the vent, and on the liver at the anterior margin of the coelom.

The head region has enlarged considerably. There is a large amount of space inside the cranial cavity leaving ample room for the brain to enlarge. The eye is very large and the choroid fissure is still present of the lower posterior portion of the eye. Two large elliptical nasal

FIGURE 16

O. ATLANTICUS LARVA (5.86 mm TL)

(mesolarval phase)



MILLIMETERS

invaginations are visible on the snout. A well developed mouth is present in a terminal position. Four large canines emerge from each side of the maxilla. There are also 2 canines on each side of the anterior lateral portion of the lower jaw.

Eight spines have grown on the posterior margin of each preoperculum. Six large stellate melanophores are present on the hyoid arch. These can be seen through the transparent preoperculum, extending from the area of attachment of the lowest branchiostegal ray, to the posterior margin of the eye. The otic capsules are indistinct but the sagitta, lapillus and asteriscus are visible. Up to 10 melanophores occur on each side on top of the head, and a large cluster of melanophores appears above the medulla oblongata.

Pectoral fins are not well developed at this stage but some rays are condensing. Numerous melanin pigments occur on the inside portion of the fleshy lobe of both pectorals. Distinct fin rays are present in the dorsal and anal fins, with clusters of melanophores visible at the base of each anal fin ray. The tail is round and 13 rays are visible. Clusters of melanophores also occur at the base of the caudal rays. Morphological measurements of similar specimens are presented in table 7 together with those of the specimen described in section 7.3.1.

The most interesting feature of this stage are the canines and the relatively small mouth. Shirota (1970) stated that relative mouth size determines food type and

TABLE 7

DESCRIPTION OF *O. ATLANTICUS* LARVAE (part II)

| FIGURE | #15 | #16 |
|-------------------------------|-----------|-----------|
| Total length of specimen (mm) | 2.78 | 5.86 |
| | (%TL) | * (%TL) |
| Notochord length | 2.66 (96) | -- |
| Standard length | -- | 5.19 (89) |
| Snout length | 0.14 (5) | 0.40 (7) |
| Eye diameter | 0.22 (8) | 0.52 (9) |
| Head length | -- | 1.40 (24) |
| Prenus length | 1.39 (50) | 2.10 (36) |
| Snout to pect. origin | 0.60 (22) | -- |
| Pectoral fin length | 0.17 (6) | 0.67 (11) |
| Depth at cleithral symp. | 0.43 (16) | 1.22 (21) |
| Snout to pelvic insert. | -- | -- |
| Pelvic fin length | -- | -- |
| Snout to dorsal spine. | -- | -- |
| Snout to dorsal ray | -- | -- |
| Snout to end of dorsal fin | -- | -- |
| Snout to anal fin origin | -- | -- |
| Snout to end of anal fin | -- | -- |
| Depth at caudal peduncle | 0.12 (4) | 0.49 (8) |
| Caudal fin length | -- | 0.79 (13) |

* The figures listed represent the means of measurements recorded on 3 specimens of similar size.

intake rate. This feature may also be an indicator of the time required from first feeding to metamorphosis (Marliave 1977). Thus, redlip blenny larvae may feed actively on small zooplankton (because of the teeth) and probably metamorphose relatively late because of the relatively small mouth. Other important features of this planktonic phase are the enlargement of the cranial region, the shortening of the preanus length and the presence of preopercular spines. Such features are common in the planktonic phases of numerous blennioid larvae reported in the literature.

8.2.2 Larval distribution and abundance

Data on the distribution, size and abundance of redlip blenny larvae, obtained from the ichthyoplankton survey, are presented in Table 8. However, these data does not lend themselves to quantitative analysis because:

A. The towing regimes used in this survey were not suitable for determining the specific distribution and abundance of larvae in both inshore and offshore waters. Insufficient time prevented me from conducting the number of tows required for accumulating such information. Most plankton tows were limited to the full moon period, and for reasons beyond my control, some tows were delayed up to 4 days. Such temporal variation in sampling allows for only limited speculation on the periodicity of larval abundance and distribution.

B. Because plankton is patchy, or overdispersed (Cassie

TABLE 8

Distribution and abundance of *O. atlanticus* larvae

| LOCATION | DATE | # LARVAE (/sample) | RANGE (mm.) | MEAN (-+S.D.) | TOTAL NUMBER (/1000 cu.m.) |
|----------|---------|-----------------------|----------------|------------------|-------------------------------|
| HOLE. | 14/5/80 | 1 | --- | 2.06 | 1.51 |
| (200m) | | 0 | --- | -- | 0 |
| (300m) | | 0 | --- | -- | 0 |
| SPEIGHT. | 14/5/80 | 0 | --- | -- | 0 |
| (200m) | | 0 | --- | -- | 0 |
| (300m) | | 0 | --- | -- | 0 |
| HOLE. | 24/5/80 | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |
| BLACK. | 30/5/80 | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |
| SPEIGHT. | 30/5/80 | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |
| HOLE. | 18/6/80 | 6 | 3.78-5.61 | 4.76(0.60) | 9.00 |
| | | 3 | 4.03-5.49 | 4.68(0.74) | 5.15 |
| | | 0 | --- | -- | 0 |
| SPEIGHT. | 19/6/80 | 1 | --- | 4.03 | 1.56 |
| | | 3 | 5.37-6.71 | 6.00(0.67) | 4.55 |
| | | 0 | --- | -- | 0 |
| BLACK. | 20/6/80 | 8 | 2.93-5.67 | 4.43(0.85) | 15.63 |
| | | 6 | 4.21-5.98 | 4.82(0.62) | 9.40 |
| | | 3 | 3.36-5.37 | 4.56(1.06) | 4.57 |
| HOLE. | 17/7/80 | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |
| BLACK. | 18/7/80 | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |
| SPEIGHT. | 19/7/80 | 0 | --- | -- | 0 |
| | | 1 | --- | 3.78 | 1.90 |
| | | 0 | --- | -- | 0 |
| BLACK. | 14/8/80 | 0 | --- | -- | 0 |
| | | 3 | 3.97-5.67 | 4.66(0.90) | 5.67 |
| | | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |

| LOCATION | DATE | # LARVAE (/sample) | RANGE (mm.) | MEAN (-+S.D.) | TOTAL NUMBER (/1000 cu.m.) |
|----------|---------|-----------------------|----------------|------------------|-------------------------------|
| HOLE. | 15/8/80 | 0 | --- | -- | 0 |
| | | 1 | --- | 3.90 | 2.26 |
| | | 1 | --- | 3.78 | 2.08 |
| SPEIGHT. | 16/8/80 | 0 | --- | -- | 0 |
| | | 1 | --- | 4.45 | 2.26 |
| | | 0 | --- | -- | 0 |
| | | 0 | --- | -- | 0 |
| HOLE. | 4/2/81 | 0 | --- | -- | 0 |
| HOLE. | 9/3/81 | 0 | --- | -- | 0 |
| HOLE. | 3/4/81 | 1 | --- | 3.84 | 2.25 |
| HOLE. | 4/5/81 | 0 | --- | -- | 0 |
| HOLE. | 1/6/81 | 37 | 3.29-5.80 | 4.60(0.69) | 78.89 |
| HOLE. | 1/7/81 | 1 | --- | 3.48 | 2.24 |
| HOLE. | 1/7/81 | 0 | --- | -- | 0 |
| HOLE. | 9/7/81 | 0 | --- | -- | 0 |
| HOLE. | 21/7/81 | 0 | --- | -- | 0 |
| HOLE. | 28/7/81 | 0 | --- | -- | 0 |
| HOLE. | 3/8/81 | 1 | --- | 6.22 | 2.57 |
| HOLE. | 10/8/81 | 1 | --- | 3.97 | 2.97 |

1968), the statistical treatment of plankton patches is difficult. Two general approaches are commonly used for this analysis: Log transformations of data coupled with parametric tests (Cassie 1962), or the use of non-parametric tests performed on untransformed data. Because of the problems outlined earlier, the small sample size and the very low means obtained, the latter method was chosen. Even though adequate, this approach will not yield as much information as the former, since no conclusions can be drawn about the distribution of samples. Nevertheless some qualitative information on the distribution and abundance of the larval stages is presented here.

Redlip blenny larvae were obtained in all three locations sampled (table 8). No comparison can be made between the larval populations of each geographical location, since simultaneous tows at each station are required for such purposes. The figures from June and August, 1980, were used independently to determine if larvae were more abundant in any strata of the water columns sampled. Results of a Kruskal-Wallis test revealed no significant difference to exist ($P < 0.05$) in the total number of larvae/1000 m³ in surface waters (0-10 m), the mid-water zone (20-20 m) and the deep water zone (35-40 m), for either period.

The same data (June 1980) were used to determine if there was a difference in the length of larvae occupying different zones in the water column. The use of a Kruskal-Wallis test

revealed no significant difference ($p < 0.05$) between the total length of larvae in surface waters, the mid-water zone and the deep water zone.

O. atlanticus larvae were not captured in surface waters at night, although they were captured on the same day in surface waters. This constitutes only weak evidence, but it does support the suggestion of Watson & Leis (1974) that blennioid larvae may undergo reverse vertical migration, that is go to deeper waters at night.

Larval blennies, ranging from 3.3 to 6.7 mm(TL), were present in nearshore waters from 13 to 24 days after full moon. The lengthy breeding period of *O. atlanticus* is responsible for the extended presence of such small larvae, and for variation in the length of specimens obtained at any specific time.

No larvae were caught in surface waters over the offshore slope of the fringing reef (0.5 km offshore), although they were caught on the same day in surface waters above the offshore slope of the bank reef (0.7-1.0 km offshore). Major differences exist between the two regions in regard to the extent of mixing in the water column. Although both regions are subject to the influence of currents running parallel to shore, the zone adjacent to the bank reef is generally subject to stronger current velocities (Ott 1975). The back and forth movement of water created by these currents stirs up bottom sediments. This zone is also enriched by a certain degree of upwelling

generated by the offshore winds.

Although quite abundant in nearshore waters, only a single young larvae was captured offshore. It may be argued that such a low figure results from the fact that offshore waters were only sampled on one day. However, many samples were taken during that single expedition and the absence of larvae in these samples may be meaningful.

It is also interesting to note that the larvae captured was the smallest specimen ever caught by the plankton net. Since the net was not effective in capturing larvae of such dimensions, it is hypothesized that there may be an abundance of these very young larvae in the vicinity of the offshore stations.

Finally, the figures on the numerical abundance of the larvae from both field seasons, indicate a definite peak in larval abundance occurs during June. Although no larvae were caught in February and March, this may be because only a single monthly sample was taken during each month.

O.atlanticus larvae probably occur in relatively low densities during these months.

8.3 DISCUSSION

The primary objective of this survey was to identify and describe the larval phases of *O.atlanticus*. It may be suggested that the fish larvae described are not redlip blenny larvae. Indeed, the only way to be certain of such

identification is to successfully rear the larvae from hatching to final metamorphosis, and until this is done, some degree of uncertainty will always prevail. However, I believe there is sufficient circumstantial evidence to support my identification. It must be kept in mind that all subsequent conclusions drawn upon the larvae described in this chapter, are based upon this opinion.

The biology of tropical marine fish larvae, particularly of reef species, is poorly understood (Leis & Miller 1976). The data on *O. atlanticus* larvae obtained during the present survey is clarified when considered in conjunction with historical and current hypotheses on the distribution and abundance of larval fishes.

The possibility that early life history events might effect the population size of adult fishes was first proposed by Hjort (1914). Both causes of larval mortality hypothesized to be important by Hjort (1914), lack of suitable food and drift of larvae, have been examined. It is now recognized that both factors operate simultaneously to influence the year class strength of populations. The importance of sufficient food of suitable size has been demonstrated in numerous experiments on the rearing of marine fish larvae, including this one. Although zooplankton diversity is high in the tropics, densities are low at low latitudes (Raymont 1963). In various tropical areas, inshore waters contain significantly more planktonic food than offshore waters (Johannes 1978). Similar increases in

production in the proximity of oceanic islands have been demonstrated. This phenomenon, termed the "island mass" effect, has been described by Raymont (1966) as a tendency towards an increase in primary production and a general rise in the standing crop of plankton in regions around oceanic islands. Constant current regimes around islands such as Barbados have the potential to carry young larvae away from these productive zones. The fact that the inshore fish fauna of Barbados is no less diverse than that of other Antillean islands indicates that larval transport between islands does occur. However, it seems unlikely that most fish larvae undergo lengthy pelagic migrations, given the low quantity of food available in offshore waters. Given these facts, it seems reasonable to look for a mechanism which might return a significant number of the larvae back to the island from which they came.

Eddy-like current patterns, potentially suitable for retaining planktonic larvae, have been observed in areas downcurrent from islands situated in constant oceanic systems. Emery (1964, 1972) noted that the distribution of benthic invertebrates corresponded to larval drift patterns predicted by the presence of a Von Karmen vortex system in the wake of Barbados. In such a system however, the eddies form, grow, break away and drift downcurrent, thus the efficacy of this system as a retention mechanism is questionable.

Sale (1970) has given evidence that a standing gyre in the

lee of Hawaiian islands could potentially retain larvae of acanthurids, but the gyre was sufficiently far downcurrent from the island to be of questionable effectiveness as a retaining mechanism. Powles (1975), on the basis of the cumulated rank score distributions of inshore fish larvae, suggested the existence of a pair of counter-rotating eddies in the wake of Barbados. He proposed that such small neritic currents could function in retaining inshore fish larvae. But Powles (1975) also noted that blennioid larvae were usually more abundant at the 45 m (depth) contour line (inshore) than at the 180 m contour (offshore). This suggests that blennioid larvae may remain close to shore, without the help of standing eddies.

Peck (1978) concluded "larval stocks are maintained off the islands west coast because of a reduction in surface wind stress in the lee of the island and also because Barbados disrupts surface drift. Thus, instead of conjecturing as to how the larvae are brought back to the west coast, it may be better to assume most of the stock is not swept downstream in the first place".

Currents near shore of oceanic islands have not been subject to much study, but appear to be slower than those of the surrounding ocean. Scattered observations in Barbados suggest that a zone of sluggish currents, not directly affected by the sweep of oceanic currents, exists near shore around the island (Powles 1975). Similar conclusions were reached by Murray et al. (1975) from their observations on

drogue movements in Barbados. It is hypothesized that these currents may assist larvae in maintaining a position close to shore.

Potentially, such a mechanism could account for the unexpected presence of large numbers of larval fishes obtained by Miller (1973), at the upstream edge of Hawaiian islands, but it does not explain why the youngest larva caught in my study, was found in offshore waters. It also fails to explain the total absence of larvae in waters closer to shore, in the inner trough, i.e., inside the bank reef.

A hypothetical migration path for *O.atlanticus* larvae is proposed here. The 'upper level swimming' behavior exhibited by redlip blenny larvae reared in aquarium showed that they remain in surface waters for the first 4 days. Since surface waters are swept offshore by prevailing winds, the larvae would be expected to be quickly transported to offshore waters. Given the feeble swimming abilities of the larvae at this stage, some kind of mechanism must assist them in maintaining a position close to the island where food abundance is greatest.

A transport mechanism was proposed by Miller (1979) to account for the unusually high abundance of tuna larvae in the nearshore waters of Hawaiian islands. Basically, Miller suggested that young fish larvae leave the surface waters and migrate to deeper waters. By leaving the wind-driven surface waters, the larvae are not swept away from the

island. From this position, maybe at the thermocline, surfaceward and shoreward transport may be accomplished by upwelling. Provided that *O.atlanticus* larvae possess the necessary behavioral attributes, the mechanism proposed by Miller (1979) would account for their distribution. Such a mechanism would have the effect of accumulating larvae near the bank reef, where they were found in relatively high abundance. Furthermore, the absence of larvae in areas closer to shore may be accounted for.

Water passing over coral reef communities is hazardous for both drifting eggs and larvae. More than 50% of the net zooplankton drifting over shallow, coral reef communities is typically removed from the water within a distance of a few hundred meters (Johannes & Gerber 1974). Furthermore, zooplankton-eating fishes in shallow waters can be an important source of predation (Emery 1968, Hobson 1974, Hobson & Chess 1978). Therefore, whereas offshore waters are relatively less productive, predation there may be reduced because such areas contain fewer planktonic, benthic and pelagic predators. The zone situated between offshore and inshore waters i.e, the outer edge of the bank reef, may offer the best compromise; sufficient quantities of food and tolerable predation pressures. Such a process could account for the observations of Miller (1973), who noted that the density and diversity of larval fish were not significantly correlated with zooplankton volumes in Hawaiian islands.

This model can also account for the presence of larger redlip blenny larvae. No larva exceeding 6.71 mm (TL) was captured with the plankton net during this survey (table 8). I believe that larger larvae were not caught by the net simply because of their ability to avoid it. Nevertheless, the exact distribution of the larger larvae is important in determining the accuracy of the migration pattern proposed. Marraro (1978) hypothesized that larger larvae migrate to deeper waters offshore of Barbados. Although results of this survey do not provide evidence to refute this hypothesis, additional information (see section 9.2.2) suggests that at least some older larvae occur over inshore waters (0-50 m). Such observations are in agreement with the model proposed.

Data on the distribution and abundance of young larvae can be used to suggest a crude estimate of growth rate. Assuming that peak spawning occurs at full moon, then peak hatching happens 4 days later (FM +4). These larvae then occur in nearshore waters between FM+13 and FM+24, or on average, 14 days later. The larvae grow from approximately 2.2 mm to 4.6 mm during this period, which represents roughly a growth rate of 0.17 mm/day.

Powles (1975) concluded on the basis of larval catches that members of most inshore reef fish families around Barbados had two peaks of abundance in the ichthyoplankton, one in March-May and one in August-October. Since the peak reproductive activity in *O. atlanticus* occurs during April-May, redlip blenny larvae would be expected to show a

spring peak in abundance similar to that of other inshore fishes. The nearshore larval catches of May 1980 and 1981 are not representative of peak egg production for the following reasons:

Most plankton tows taken during May, 1980, were not done in the period during which young larval stages are normally found in nearshore waters (FM+13 to FM+24). It is assumed that larval catches similar to those of June would have been obtained had tows been taken during the new moon period of May.

No redlip blenny larvae were caught during May 1981 in the plankton tows. However, it is assumed that the underlying cause responsible for such figures concerns the state of the parent population at that time of the year. Figure 22 (section 10.3) reveals that the population density during April, 1981, was at a record low. This, in turn, translated into a low production of larvae which accounts for the absence of the expected spring peak of larval abundance in nearshore waters.

From this survey, no conclusions can be drawn as to the presence of a peak in larval abundance during the fall such as Powles (1975) observed for most inshore fishes. Should such a peak be observed, it would certainly not be induced by a peak in reproductive activity, since that period of the year corresponds to the low reproductive period in the blenny population. Fluctuations in larval catches and recruitment due to variations in hydrographic conditions are

debated in chapter 9.

9. RECRUITMENT

There is some information in the literature concerning the recruitment pattern of *O.atlanticus*. Springer (1962) has suggested that the larvae of *O.atlanticus* do not undergo direct development. Marraro (1978) hypothesized that large, unmetamorphosed larvae (35-40 mm TL), two to three months old, settle out of the plankton at a fairly late stage of development. He also speculated that transformation and metamorphosis of the pelagic forms is induced by substrate contact and occurs within the crevices of the reef structure. The author observed a seasonal peak in recruitment (early to mid summer) and concluded that there was year round recruitment of *O.atlanticus* larvae to Barbados. Finally, Nursall (1977) demonstrated that small immature redlip blennies take up 'interstitial' territories between the adults and proposed that these 'interstitial' territories are expanded as the blenny grows.

In the present study, 3 different investigations were used to obtain additional information on the recruitment pattern of *O.atlanticus*. The information concerning each method is outlined below.

9.1 Materials & Methods

9.1.1 Investigation I

Between May and August 1980, juvenile fishes were captured using experimental fish traps. Each trap consisted of a rectangular frame (60 cm X 60 cm X 30 cm) made of tubular P.C.V pipes (2.2 cm OD). The whole structure was covered with black nylon mesh having rhomboidal openings (9.5 X 1.5 mm). A second layer of screen with 1 mm² openings was attached to the bottom of the cage. Thus each side of the cage, except for the base, would allow fishes smaller than large adult blennies to enter or leave the enclosure. All cages were filled with pieces of live and dead coral (*Porites porites*, *Millepora* sp., *Monastrea annularis*, etc.) and placed at different locations on Heron Bay reef, approximately 1 km north of the Bellairs Research Institute.

The first series of cages was positioned on the top, sides and bottom of coral heads occupied by redlip blennies. Site A consisted of a small coral head in 1 m of water. One cage was placed on the top of the head while a second cage was placed on the bottom adjacent to the coral head. Adult blennies were present in both positions prior to the delivery of the cages. Site B consisted of a coral head 1.5 m in height, situated in 2.5 m of water. Cages were placed on the top, the side and the base of this coral head. Adult blennies were also seen at these positions prior to the delivery of the cages. Site C consisted of a large coral

formation in 4 m of water. Cages were placed on the top, the side and the base of this formation at depths of 2, 3 and 4 m respectively. Only a few redlip blennies were present at the top of the coral formation prior to the delivery of the cages. Because of the strong currents prevailing in this area, all cages were tied to the substrate with nylon rope.

A second series of cages was placed over an open area, at two different depths (2 and 3 m), to appear as isolated coral heads. At each position two cages were placed on top of a metal rack of 'Dexion' pieces, and an additional pair was also placed under the metallic structure, in contact with the bottom (plate 5). The idea here was to provide a larger living space and to increase the height of the structure in relation to the bottom. Redlip blennies are not observed very often on small isolated pieces of coral, but have been observed to hold territories on isolated coral heads of dimensions similar to this experimental recruitment site.

Due to the time involved in building, testing and checking the structures, not all cages were positioned simultaneously. The first enclosures were placed on May 18, and the number of cages *in situ* increased to a total of 16 by August, 1981. The final position of the cages is shown in Fig. 17.

Once in position, each cage was checked every second week for the presence of recruits as follows: the cage was untied and put inside another metallic cage having a mesh

PLATE 5

Underwater enclosures of Heron Bay



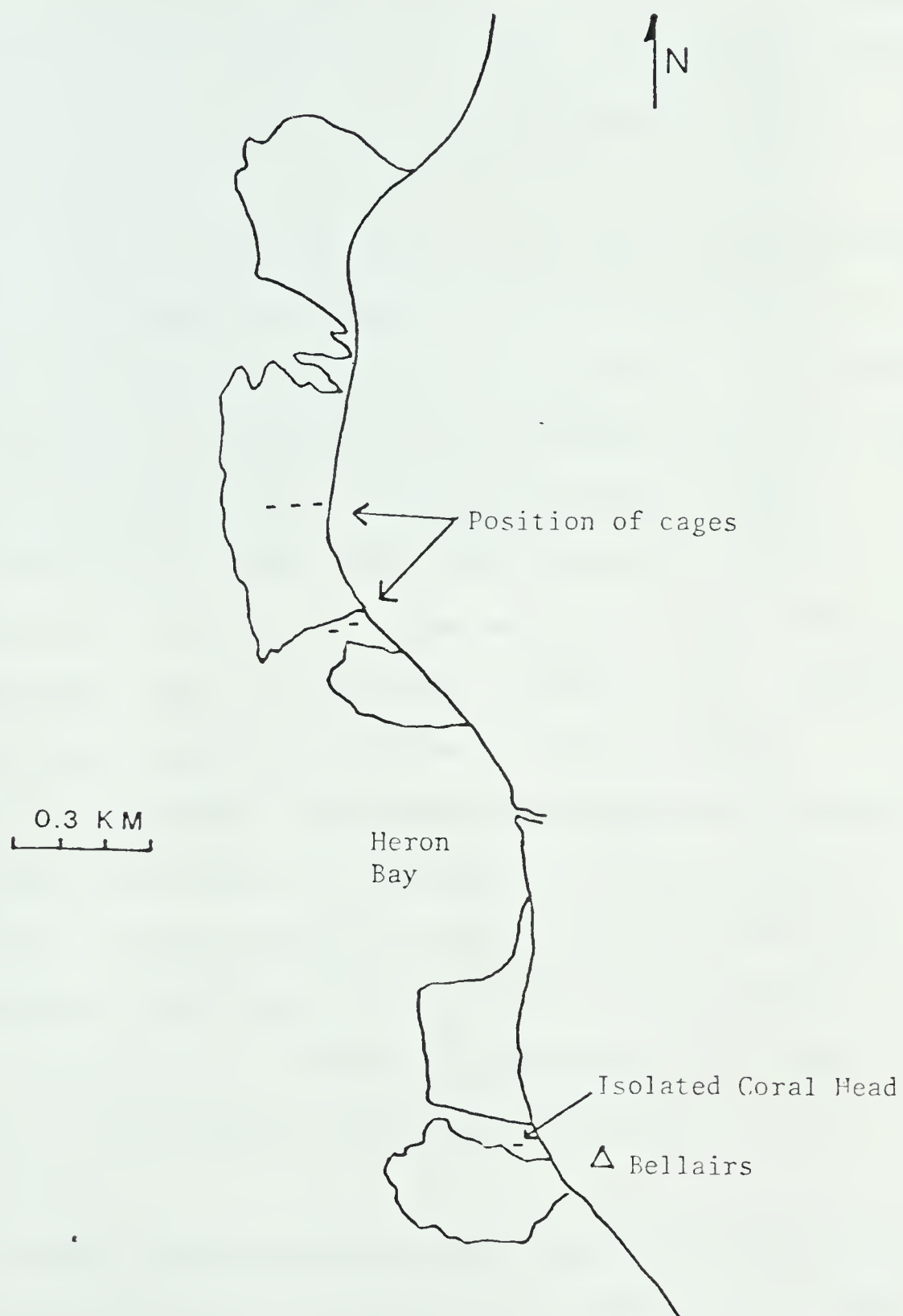
size of 1 mm². The combined structure was then brought up to the surface. This procedure eliminated the risk of losing small fishes during while manipulating the cage. Once in the boat, all fishes in the cage were measured (total length in mm) and placed in numbered jars containing a 5% formalin solution. The coral rubble was replaced with 'new' substrate material, algae was brushed off the nylon mesh and the cage was put back in its original position. This investigation was terminated on August 3rd, 1980, because all cages were destroyed during Hurricane Allen.

9.1.2 Investigation II

During January and February 1981, small fishes were collected weekly under a light suspended in the water at night, at the end of the steel pier in front of the Coral Reef Club adjacent to the Bellairs Research Institute. In this position, I was situated above 2 m of water (at high tide), at the edge of a large coral formation next to a large sand patch. A diver's light was attached to the pier under the water and the larvae attracted were captured with a large dipnet (0.25 m²). All fishes captured were brought back to the lab, measured and preserved in 5% formalin solution for future identification.

FIGURE 17

POSITION OF EXPERIMENTAL ENCLOSURES ON HERON BAY REEF



9.1.3 Investigation III

From January to August, 1982, recruitment was investigated through the use of rotenone. An isolated coral head in front of the Bellairs Research Institute was arbitrarily chosen as an experimental study site. This head was 1.5 m high, 2.2 m wide and 2 m deep. It was positioned in 3 m of water on a sand patch, surrounded by a large coralline formation.

Once a week, between 9:00 and 12:00 AM, I would descend to the head and inject rotenone into the crevices of the coral head. The rotenone dispenser consisted of a hot water bottle coupled to a hollow aluminum tube by a piece of Tygon tubing, and equipped with a oneway valve and a nylon stopper. With this device, I was able to control the distribution of the solution injected. After injection, all fishes emerging from the head were captured with a handnet. Most fishes were caught during the first 10 minutes following the injection. No fishes were observed to emerge from the head later than 15 minutes following injection. Nevertheless, I would remain at the site for at least 20 minutes before returning to the lab with the fishes caught. In the lab, all fishes were measured (TL) and preserved in a 5% formalin solution for future identification.

All fishes captured during each sampling session were kept in the laboratory in numbered containers. The fishes were always identified to genus or, if possible, to species.

PLATE 6

Author sampling fauna from isolated coral head



All classifications were done on the basis of the keys of Bohlke & Chaplin (1968). After classification, most fishes were sent either to the Royal Ontario Museum (Toronto, Canada), the museum of the University of Alberta (Edmonton, Canada) or the museum of the Underwater Park of Barbados (Holetown, Barbados). All records of catches were kept for further reference.

9.2 RESULTS

9.2.1 Investigation I

The experimental fish traps used in this investigation were quite successful in capturing small fishes. Juveniles and small adults of most families of inshore fishes (Scaridae, Pomacentridae, Clinidae, Gobiidae, Gobiesocidae, Labridae, Muraenidae and others) were caught in large numbers throughout the experiment. Such results were anticipated, since the enclosures were designed to reduce predation upon larval fishes recruiting to the reef. However, by and large, this experimental approach yielded very little information on the recruitment pattern of the redlip blenny. Data on the catches of redlip blennies is presented in Table 9.

Pre-metamorphic larval blennies were described by Springer (1962) as possessing torpedo-like bodies, forked tails and large canines on the upper and lower jaws. Only

TABLE 9

DETAILS OF REDLIP BLENNY CAPTURES

| DATE | F.M. | SIZE (TL. mm) | TYPE | LOCATION |
|----------|------|------------------|-------|----------|
| 18/06/80 | +20 | 77 | adult | A-top |
| | | 75 | adult | A-top |
| | | 49 | juv. | A-top |
| | | 44 | juv. | A-top |
| 23/06/80 | +25 | 40 | juv. | B |
| 2/07/80 | +4 | 70 | adult | A-top |
| | | 44 | juv. | A-bottom |
| | | 40 | juv. | A-top |
| 9/07/80 | +11 | 41 | juv. | B |

Definitions:

Juv.= Juvenile blenny as described in text.

F.M.= Number of days elapsed since full moon.

TL = Total length.

top = Top of coral head

side= Side of coral head

bottom= Bottom of coral head

A & B = Indicate the position of the cages as defined previously.

one of these characteristics (the forked tail) was observed in the smallest blenny captured (40 mm). All other small individuals (40-49 mm) were almost identical in appearance to the adults, except for the poorly developed genital papillae. Therefore, these small larvae were arbitrarily designated as juveniles.

All juveniles were captured in zones normally occupied by adults. No noticeable differences were found between the total number of blennies caught in Zone A and Zone B. No juveniles or adults were ever caught at the deeper stations furthest from shore (zone C in 4 m of water).

9.2.2 Investigation II

Larvae, juveniles and adults of several species of reef fishes, were captured throughout the month during January and February, 1981. Only a single larval fish was found to resemble the description of *O.atlanticus* provided by Springer (1962). It was caught on January 26th (FM +6) at 9:30 P.M., and was positively identified as a redlip blenny larva (advanced mesolarva). The specimen is illustrated in Fig. 18.

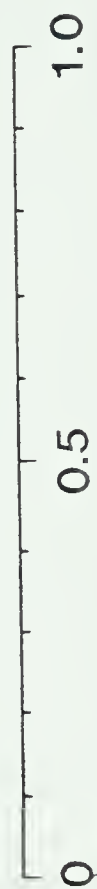
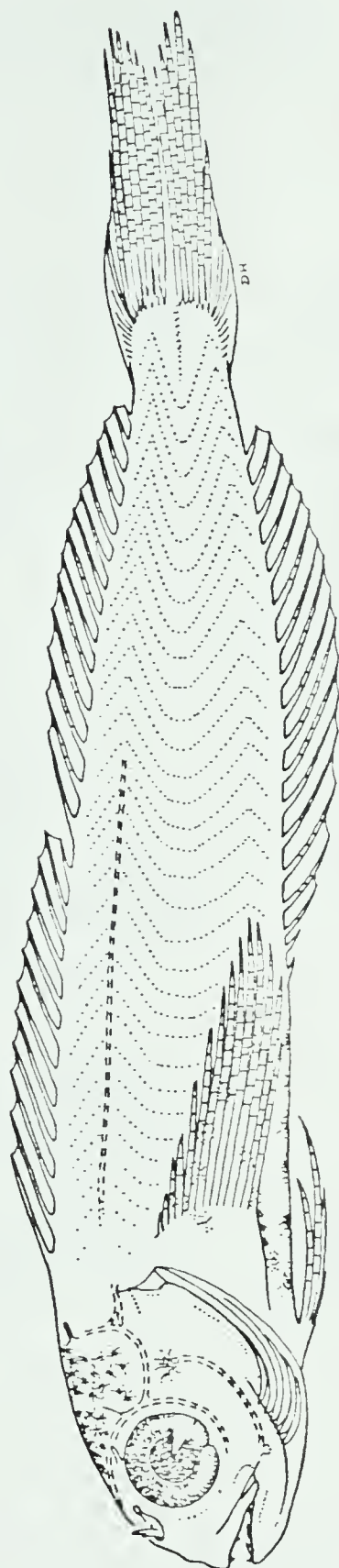
Morphometric data of this specimen (19.64 mm TL) are presented in Table 10, along with those of the younger larvae (5.86 mm TL) described in section 8.2.1 (Fig. 16).

The most noticeable difference between this specimen and that in Fig. 16 concerns the development of fin elements. In this specimen, the dorsal fin consist of 12

FIGURE 18

O. ATLANTICUS LARVA (19.64 mm TL)

(advanced mesolarval phase)



CENTIMETERS

TABLE 10

DESCRIPTION OF *O. ATLANTICUS* LARVAE (part III)

| Figure | #16 | #18 |
|-------------------------------|-----------|------------|
| Total length of specimen (mm) | 5.86 | 19.64 |
| | (%TL) | (%TL) |
| Notochord length | -- | -- |
| Standard length | 5.19 (89) | 15.56 (80) |
| Snout length | 0.40 (7) | 0.82 (4) |
| Eye diameter | 0.52 (9) | 1.22 (6) |
| Head length | 1.40 (24) | 3.54 (18) |
| Preanus length | 2.10 (36) | 7.32 (37) |
| Snout to pect. origin | -- | -- |
| Pect. fin length | 0.67 (11) | 3.78 (19) |
| Depth at cleithral symp. | 1.22 (21) | 3.05 (16) |
| Snout to pelvic insertion | -- | 3.05 (16) |
| Pelvic fin length | -- | 2.75 (14) |
| Snout to dorsal spine. | -- | 3.78 (19) |
| Snout to dorsal ray | -- | 9.15 (47) |
| Snout to end of dorsal fin | -- | 14.34 (73) |
| Snout to anal fin origin | -- | 7.50 (38) |
| Snout to end of anal fin | -- | 14.03 (71) |
| Depth at caudal peduncle | 0.49 (8) | 1.16 (6) |
| Caudal fin length | 0.79 (13) | 0.98 (5) |

spines and 14 segmented unbranched rays. There is a definite separation between the two portions of the dorsal fin. The anal fin contains 2 short spines and 16 unbranched rays. Each pectoral has 14 simple rays. The pelvics have 4 simple rays, the innermost of which is much shorter and more slender than the others. The caudal fin is forked, with 7 unbranched rays above and 6 below. Only the caudal and pelvic fins have the same number of rays as found in the adults.

The vertebral column, with 33 vertebrae has grown considerably in relation to other body parts. This has the effect of making all parts of the body (except the pectoral fins) appear smaller (in %TL). The head is laterally compressed and relatively small but well-developed. A choroid fissure is still present on the lower posterior portion of both eyes. Two cirri occur on the margin of each anterior nostril and a single cirrus is visible on top of each eye and on each side of the nape. Dentition is characterized by two outwardly and posteriorly curved canines on each side of the anterior margin of the lower jaw. There is also an upwardly and posteriorly curved canine on each side of the lower jaw, well-separated from the anterior canines. Four downwardly and posteriorly curved canines are located under the lip of the upper jaw. Rows of comblike teeth are present along both the upper and lower jaws.

All melanophores on the cheeks have disappeared, except for one dark ocellus behind the eye. Preopercular spines, present on younger larvae (Fig 16.) have almost entirely disappeared. At the base of each operculum, six well-developed branchiostegal rays are visible. A lateral line in the dorsal portion of the body, extends posteriorly from above the fleshy lobe of the pectorals, to halfway along the body.

The color of this specimen changed after preservation. While fresh, the specimen appeared transparent and its vertebrae, blood vessels and nerve cord were clearly visible. The peritoneum was silvery and dotted by a dozen large black chromatophores. Numerous melanophores occurred on top of the head and several red pigment cells were visible in the pectoral fins. After preservation, the body acquires a milky color, and all pigments appear brown, except for those of the pectoral fins, which disappear.

9.2.3 Investigation III

Large *O. atlanticus* larvae, in various phases of development, were captured through the use of rotenone. Based on the appearance of the larvae at the time of capture, I arbitrarily defined 3 stages of development. These are presented in Plate 7 and 8. The unpreserved post-larvae (metalarval phase) are typically transparent, with the vertebrae, nerve cord and blood vessels clearly visible. The extensive peritoneum is

PLATE 7

O. ATLANTICUS post-larva (metalarval phase, above),
and pre-juvenile (below)



PLATE 8

Juvenile (above) and pre-juvenile (below)
of *O.atlanticus*



silvery. Dense pigmentation is present at the base of the spines and rays of the dorsal, anal and caudal fins. Red, brown and silver pigments occur on the head region. Four cirri are present on the margin of each anterior nostril, a single cirrus above each eye and a pair of cirri on each side of the nape.

The large canines on each jaw are covered by the lips and are not all visible externally. Those on the lower jaw have migrated to its front margin and are now curved upwards and posteriorly. The canines on the upper jaw are also situated at the anterior margin of the jaw and are curved downward and posteriorly. An additional canine occurs about halfway along the lower jaw on each side.

At this stage, the fin ray count is identical to that of the adult: dorsal rays XII,19; anal rays II,21; pectoral rays 15; pelvic rays I,4 and caudal rays 13. There is no longer a definite separation between the two portions of the dorsal fin but the tail is forked.

A typical post-larva (metalarval phase) is illustrated in Fig. 19. Morphometric data of this specimen (48.98 mm TL) are presented in Table 11, with those of a younger stage (19.64 mm TL, Fig. 18), to show major changes.

Larvae are recognized as pre-juveniles, from the time of appearance of reddish brown color on the body, until the silvery peritoneum is no longer distinguishable externally. Throughout this stage, there appears to be a gradual blunting of the head and an upward migration of the eyes. The

FIGURE 19

O. ATLANTICUS POST-LARVA

(advanced metalarval phase)

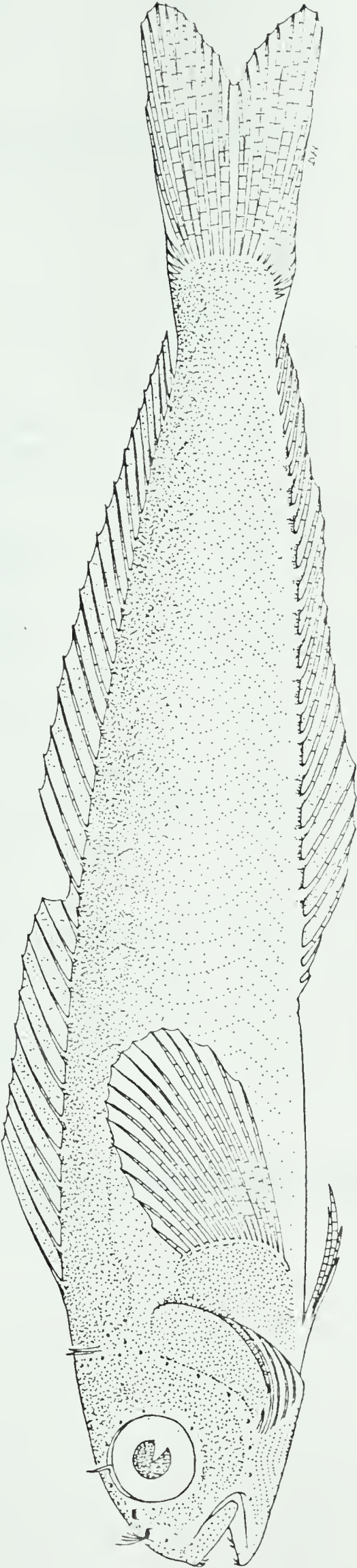


TABLE 11

DESCRIPTION OF *O. ATLANTICUS* LARVAE (part IV)

| Figure | #18. | #19. |
|-------------------------------|------------|------------|
| Total length of specimen (mm) | 19.64 | 48.98 |
| | (%TL) | * (%TL) |
| Notochord length | -- | -- |
| Fork length | -- | 46.61 (95) |
| Standard length | 15.56 (80) | 39.50 (81) |
| Snout length | 0.82 (4) | 2.05 (4) |
| Eye diameter | 1.22 (6) | 2.84 (6) |
| Head length | 3.54 (18) | 9.48 (19) |
| Preanus length | 7.32 (37) | 18.17 (37) |
| Snout to pect. origin | -- | -- |
| Pect. fin length | 3.78 (19) | 6.86 (14) |
| Depth at cleithral symp. | 3.05 (16) | 7.90 (16) |
| Snout to pelvic insertion | 3.05 (16) | 7.90 (16) |
| Pelvic fin length | 2.75 (14) | 5.69 (12) |
| Snout to dorsal spine. | 3.78 (19) | 8.85 (18) |
| Snout to dorsal ray | 9.15 (47) | 21.33 (44) |
| Snout to end of dorsal fin | 14.34 (73) | 37.92 (77) |
| Snout to anal fin origin | 7.50 (38) | 18.96 (39) |
| Snout to end of anal fin | 14.03 (71) | 37.60 (77) |
| Depth at caudal peduncle | 1.16 (6) | 2.84 (6) |
| Caudal fin length | 0.98 (5) | 8.69 (18) |

* The figures listed represent the means of measurements recorded on 3 specimens of similar size.

upper and lower marginal canines are lost but the inside canines on the lower jaw remain. The rest of the body is identical to that of other metalarvae.

Post-larvae are recognized as juveniles once they have acquired the coloration and morphology of adults, and are recognized as adults once they engage in mating (>69 mmTL).

All specimens obtained from the isolated coral head are listed in Table 12. Data on the captures is shown in Fig. 20. This information indicates that recruitment is a continuous process, between January and July, but does not occur in August. There is a definite peak in recruitment during June and July. Finally, the data indicates that recruitment occurs predominantly around the new moon period.

9.3 DISCUSSION

If full development of fin elements marks the end of the larval and the beginning of the juvenile stage, then the capture of a rayless 19.64 mm redlip blenny near the shore is evidence these fish spend a part of their larval life over inshore waters. In fact, they may spend an extensive part of their existence in this area since inshore migration probably starts when the larvae reach a size of 6.7-19.6 mm and terminates at recruitment (40-46 mm).

Such conclusions are not unexpected. Sander & Steven (1973) showed that, in Barbados, zooplanktonic dry weight and wet volume are consistently greater inshore than offshore. Large

TABLE 12

FISHES CAPTURED ON ISOLATED CORAL HEAD

| DATE | LUNAR DAY (*) | O.A. LARVA (TL mm) | DEVELOP. STAGE | OTHER FISHES |
|----------|------------------|--------------------------------------|--|-----------------|
| 26/01/81 | +6 | 47.7 59.8 | pre-juv. adult | -- |
| 01/2/81 | +12 | 48.0 | pre-juv. | 14 (7) |
| 09/2/81 | +20 | none | | 35 (9) |
| 16/2/81 | +27 | 48.0 | | -- |
| 23/2/81 | +5 | none | | none |
| 02/3/81 | +12 | none | | 9 (5) |
| 09/3/81 | +19 | -- | | -- |
| 16/3/81 | +26 | 42.0 | pre-juv. | 23 (15) |
| 23/3/81 | +4 | none | | 10 (5) |
| 30/3/81 | +10 | -- | | -- |
| 07/4/81 | +18 | 43.0 | pre-juv. | 6 (4) |
| 14/4/81 | +25 | 43.0 | juv. | 2 (2) |
| 20/4/81 | +1 | none | | 3 (4) |
| 27/4/81 | +8 | 45.0 | pre-juv. | 4 (8) |
| 04/5/81 | +15 | 45.0 | juv. | 15 (6) |
| 11/5/81 | +22 | none | | 10 (4) |
| 18/5/81 | +29 | none | | 4 (2) |
| 25/5/81 | +6 | none | | none |
| 01/6/81 | +13 | 46.0 44.2 45.0 | post-l. post-l. post-l. | 10 (3) |
| 08/6/81 | +20 | 40.0 41.0 49.0 47.0 44.0 | post-l. post-l. juv. juv. juv. | 10 (5) |
| 15/6/81 | +27 | none | | 2 (2) |
| 22/6/81 | +5 | none | | 8 (6) |
| 29/6/81 | +12 | none | | 9 (4) |

| DATE | LUNAR DAY | O.A. LARVA (TL mm) | DEVELOP. STAGE | OTHER FISHES |
|---------|-----------|-----------------------|-------------------|-----------------|
| 06/7/81 | +19 | 48.0 | pre-juv. | 10 (5) |
| | | 50.0 | pre-juv. | |
| | | 47.0 | pre-juv. | |
| | | 47.0 | pre-juv. | |
| | | 52.0 | pre-juv. | |
| | | 53.0 | pre-juv. | |
| 13/7/81 | +26 | 42.0 | pre-juv. | 15 (9) |
| | | 43.0 | pre-juv. | |
| | | 44.0 | pre-juv. | |
| | | 46.0 | pre-juv. | |
| 20/7/81 | +3 | none | | 8 (4) |
| 26/7/81 | +9 | none | | 13 (8) |
| 04/8/81 | +18 | none | | 8 (6) |
| 10/8/81 | +24 | none | | 2 (1) |
| 17/8/81 | +2 | none | | 3 (3) |

Definitions:

For examples, refer to plate 7 and 8.

Figures under the "Other fishes" column refer to the total number of other fishes captured (first number) and the associated number of genera represented (in parenthesis).

-- = No data available.

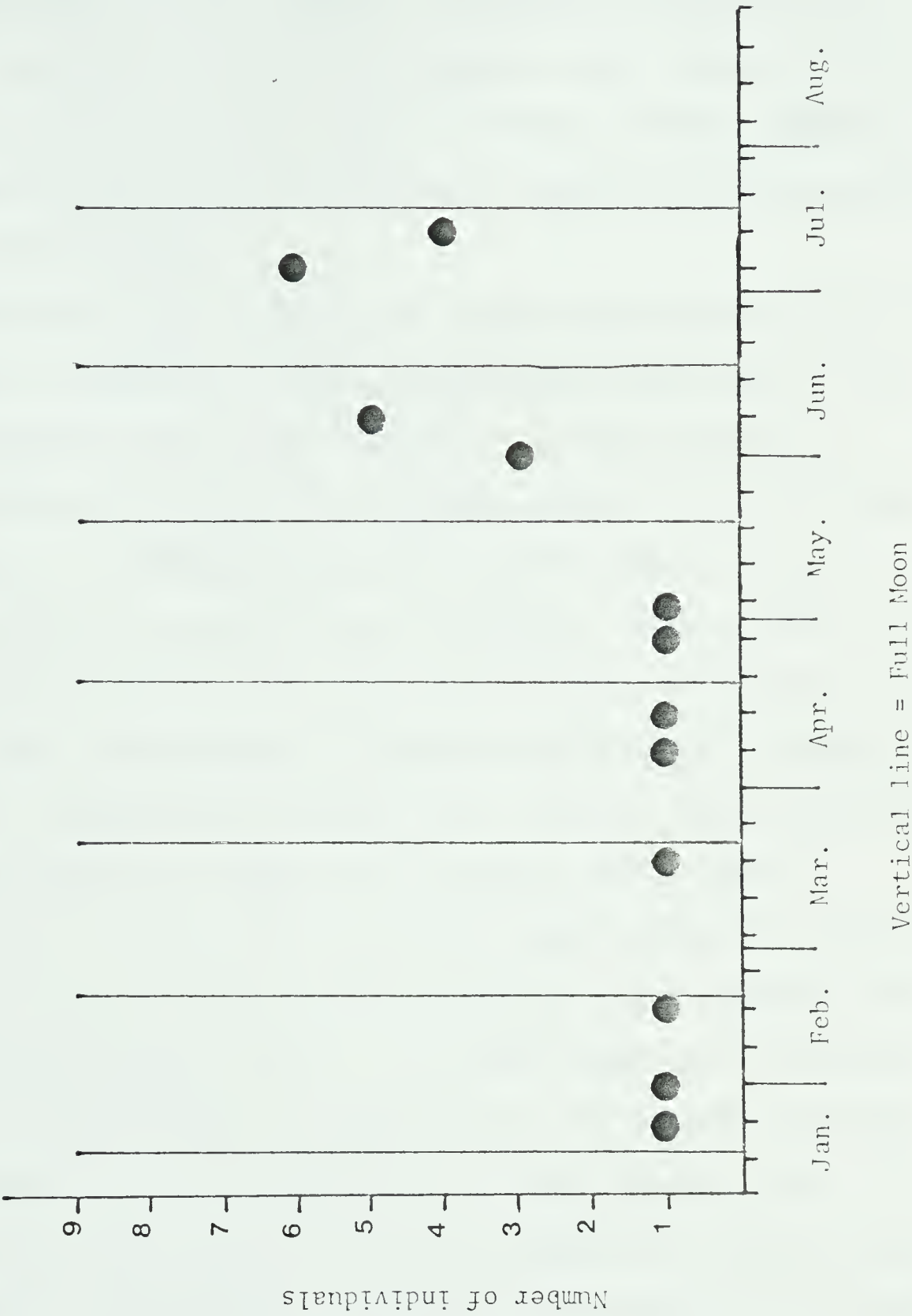
(*) FM 0 = full moon

FIGURE 20

CATCHES OF RECRUITED *O. ATLANTICUS* LARVAE AT STUDY SITE
(1981)

Small vertical bars below Y-axis represent weekly sampling intervals.

Tall vertical bars above Y-axis correspond to full moon periods.



redlip blenny larvae probably migrate to inshore waters to take advantage of this greater abundance in food, which in turns, translates into faster growth rates. Data on larval catches (4.60 mm at FM+18 and 19.64 mm at FM+6) suggests that the larvae grow at an average rate of 0.84 mm per day during this period.

The exact distribution of larger individuals (19.64 to 40-46 mm) is unknown. These larvae were never seen in the daytime while I was scuba diving in inshore waters. I believe that they migrate to deeper waters in the daytime, and return to surface waters to feed at night. Once the larvae attain a certain size (40-46 mm), they settle out of the plankton during the night and take up residence on the reef. Other investigators studying recruitment patterns in tropical fishes have observed that larval fishes settle out of the plankton at dusk (Myra Shulman, pers. comm.)

Table 12 indicates that recruitment generally occurs between 13 and 20 days after full-moon. This suggests that large *O.atlanticus* larvae (>19.64 mm) grow at an average rate of approximately 2.20 mm/day (or on average 7% body length/day) until recruitment. It also suggests that the duration of the larval life of *O.atlanticus* is approximately 1.5 months, during which time the larvae grow at an overall rate of 0.91 mm/day. Such growth rates are similar to those of tropical clupeids which range from 0.5 to 1.0 mm per day. (Houde & Palko, 1970; Saksena & Houde, 1972). Growth rates of 0.3 to 0.8 mm per day have been recorded in several

subtropical species (Houde 1974).

Most tropical marine fishes are thought to have relatively short larval lives, in the order of three to four weeks (Powles, 1975; Luckhurst & Luckhurst 1977). Many such fishes (Grammatidae, Apogonidae, Sciaenidae, Pomacentridae, Gobiidae and Canthigasteridae) return to the reef while still small (<20-25 mm TL). On the other hand, redlip blennies recruit at a fairly large size (40-46 mm) and consequently have a longer pelagic existence. It should be noted that members of the families Muraenidae, Holocentridae, Acanthuridae and Chaetodontidae are also believed to have larval lives of some 2 months duration (Marshall 1963).

Figures concerning the length of pelagic life of the larvae, estimated on the basis of this investigation, are in accord with the estimates proposed from another investigation. Several young juveniles were sent to Dr. E. Brothers at Cornell University for aging. By examining the otolith microstructure with a scanning electron microscope, Dr. Brothers concluded that *O. atlanticus* had a pre-settlement age of 28-29 days. Such figures are not identical with those obtained in the present investigation. This is believed to be an effect of the methodology used by Dr. Brothers. The usual technique used to age tropical fish is based upon the number of diel lamellae deposited on the sagitta (Ralston, 1976), and is recognized as being fairly accurate in aging adult fishes. However, the technique used

by Dr. Brothers depends upon the number of increments on the lapillus, which he believes, indicates the age of the larva. I observed that the lapillus is developed in redlip blenny larvae greater than 4.0 mm (TL), or approximately two weeks of age. Assuming that daily growth increments are deposited on the otolith after this stage, one would calculate the larval life of *O. atlanticus* to be 1.5 months, as predicted from this investigation.

By periodically sampling one isolated coral head, one obtains only limited information on the recruitment pattern of fishes. In order to understand more about such a process, other areas were sampled with rotenone. Every time I obtained recruits from the isolated coral head, I would sample an area of approximately 3 m² on the reef, in zones corresponding roughly to the locations of the experimental enclosures. This information has not been tabulated because it contains no quantifiable results which could be used to refine earlier estimates. However, 3 important observations are reported here:

I. In all instances where recruits were obtained from the isolated coral head, they were also collected the next day in other areas of the reef, and vice versa. This indicates that the use of a small isolated coral head was adequate for monitoring recruitment of *O. atlanticus* to the fringing reef.

II. The presence or absence of adults in zones sampled with rotenone did not affect the number of recruits found in

that area. Therefore, it appears that the presence of adults in the vicinity of the recruitment site is not a requirement for the recruitment of larvae. Similar processes have been reported in pomacentrids. Sale (1980) observed that juvenile stages of *Pomacentrus wardi* do not tend to recruit, more often than expected, adjacent to adults or to sites previously occupied by their own species.

III. The distribution of recruits was almost identical to that of adults. No recruits were ever found in crevices on the reef at depths exceeding 4 m, nor were they ever found in the sand: this indicates that larvae do not migrate back to the reef by following the bottom and inhabiting crevices in coral formations encountered along the way. Rather, it suggests that they can probably detect the right habitat before they settle out of the plankton and take up residence on the reef. The exact mechanism accounting for such homing process remains to be determined.

Since the isolated coral head was sampled every week, all recruits captured there are believed to be no more than seven days old (post-settlement age). Because juveniles were occasionally captured there, complete transformation from larva to juvenile must take place within a period of seven days. This can explain why no post-larvae were caught in the enclosures. By the time these were checked (every 14th day), the larvae had probably metamorphosed into juveniles.

The largest larva of *O. atlanticus* recorded by Springer (1962) was 58 mm, while the smallest metamorphosed specimen

was slightly less than 32 mm. This may suggest that during metamorphosis, there is gradual shrinking of the body. The smallest juvenile obtained in this investigation was 38 mm (TL), and the smallest post-larva 40 mm (TL). Based on these figures, I hypothesize that some decrease in size may occur during metamorphosis but it is probably not very extensive. It appears that the energy required for metamorphosis is not derived from catabolism of body tissues. Dissected post-larvae had enlarged livers. Further investigation (J.R. Nursall, pers. comm.) showed the presence of large fat deposits in the liver, which decreased throughout metamorphosis. It is assumed that the larvae derive enough energy to metamorphose by using these fatty deposits.

Data in table 12 show that recruitment occurs mostly between FM+13 and FM+20 thus, on average, recruitment is centered around the new-moon period. Recruitment was fairly constant between January and May, peaked during June and July, and was completely absent during August. To best understand such a pattern, it is necessary to review some facts on the life history stages of *O.atlanticus*.

It has been established that redlip blennies spawn year-round, with a peak occurring during April and May. I have speculated that nearshore processes facilitate the retention of larvae during their pelagic existence of 1.5 months. After this period, they they take up residence on the reef and metamorphose into adults. Based on such facts, one would expect year-round recruitment to occur, with a

peak during the new moon period of June and July, just as was observed in this study (Fig. 20). However, the absence of recruitment during August cannot be accounted for by the above information. I believe that such disruption of the normal recruitment process may be induced by the hydrographic and atmospheric conditions prevailing during August at Barbados.

In an attempt to account for variation in recruitment in several tropical fishes, Johannes (1978) concluded "it might prove revealing to compare the relative strengths of prevailing currents and winds during years of high and low recruitment". During the present investigation, no information was recorded on the direction and velocity of the prevailing winds. Nevertheless, I hypothesize that these factors may influence the recruitment of *O. atlanticus* larvae to the island. Powles (1975) also concluded that the bilobed distribution of inshore fish larvae in the lee of Barbados might be the result of rapid wind driven transport of larvae. Although offshore current patterns around Barbados do not fluctuate much throughout the year, hydrographic conditions at Barbados change drastically during the year. Between February and September, the conditions around Barbados are profoundly affected by the Amazon river outflow. Steven & Brooks (1972) showed that a series of separate eddies are formed north of the Amazon mouth during the first half of each year, which drift northwest as far as the Lesser Antilles. Measurements by these investigators

showed that these short-lived fresh water eddies have their greatest impact on surface salinity (0-25 m) between mid-July and September at Barbados.

Ryther et al. (1967) found nitrate, phosphate and phytoplankton concentrations to be lower in these low salinity lenses than in surrounding water. Such fresh water masses can have a profound effects on the surface communities of the Lesser Antilles. Lewis & Fish (1969) found seasonal variations in the zooplankton fauna to occur in Barbados, and concluded that such variation was more likely to correlate with local variations in hydrographic conditions, than with seasonal changes in production. Changes in surface waters are also accompanied by changes in the position of the thermocline . Steven, Brooks and Moore (1970) showed the thermocline to migrate upward (>150 m to 15-35 m) from January to August, and to migrate downward to its initial position between August and January.

I hypothesize that larval fishes may respond to these environmental changes in such a way that normal recruitment is interrupted. This disruption may limit, or prevent, recruitment from occurring in August. Further investigations are required to determine the nature of the relationships between the stability of environmental conditions and the periodicity of spawning and recruitment.

10. DEMOGRAPHIC STUDIES

Most investigations of population structure in reef fishes fail to interpret the observed changes in numbers, since most factors controlling population size are not monitored adequately. As a result, there has been much speculation about the stability of coral reef fish populations, which in turn has catalyzed debates on the ultimate factors responsible for species diversity and stability (for example, see discussion by Sale 1977). Serious contradictions remain in this regard; Smith & Tyler (1972) claimed that there is no evidence of large fluctuations in abundance of reef fishes during the year, while Australian biologists have observed dramatic fluctuations in species composition in small areas of reef (Ehrlich 1975).

During this investigation, I attempted to obtain some information on the stability of the redlip blenny population of Barbados.

10.1 MATERIALS & METHODS

A survey of the numerical abundance of the population was carried out from May to September, 1980, and from February to September, 1981.

A first transect was established at the end of Heron Bay (see chapter 4 for details) and was patrolled at least every week during the above periods. A second transect (1.0

m X 100 m) was established during February 1981 in a similar zone, 1.5 km north of Heron Bay on the west coast of Barbados, and was also patrolled at least every week until August 1981.

All censuses were made in the following manner: I would swim slowly (0.75-1.0 m/minute) at the surface and record the total number of redlip blennies seen in the transect.

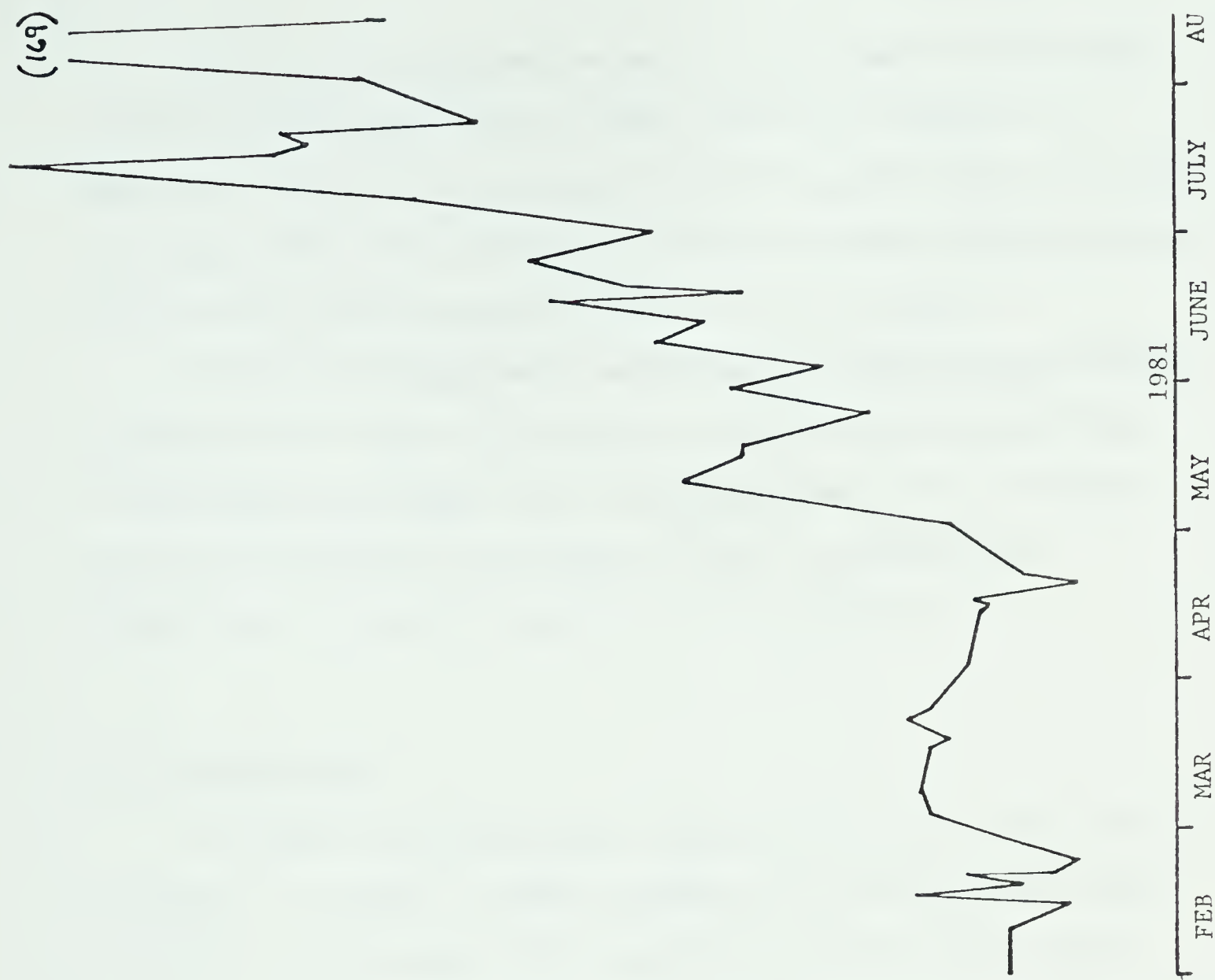
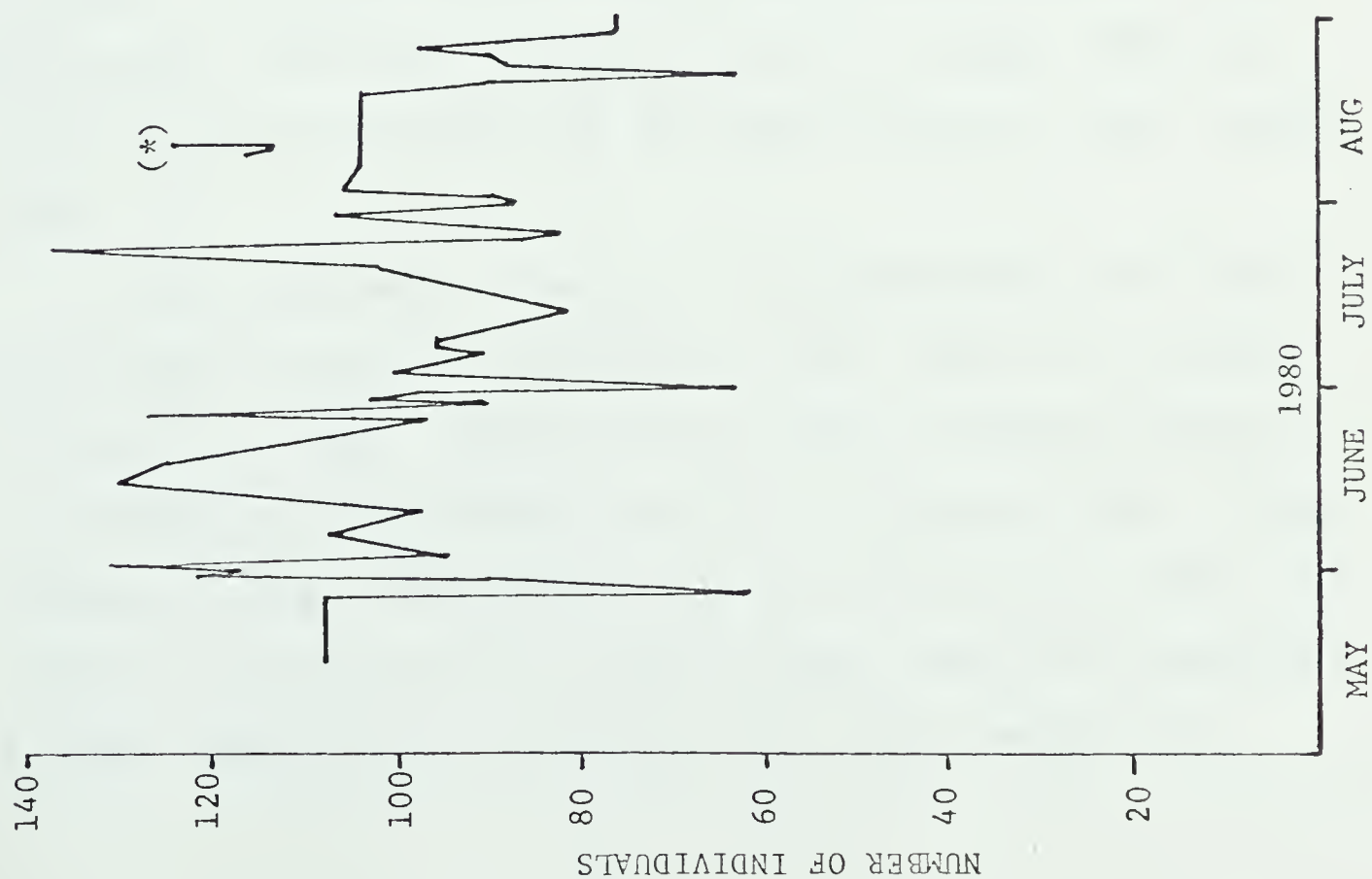
10.2 RESULTS

Results of the population census at Heron Bay (transect A) are presented in Fig. 21. The data obtained during 1980 show that the population remained at a fairly constant level during that summer even though the number of individuals observed varied considerably throughout this interval (from 60 to 140). Monthly peaks in abundance were induced by the recruitment of juveniles to the study site. High mortality and poor visibility are believed to be the main factors responsible for the low values. Smaller fluctuations are attributed to immigration and emigration of individuals from the study site at the time when the census was made. An average density of 1.67 redlip blennies per m² was calculated on the basis of this data. This observation is similar to Nursall's (1981), who reported the density of redlip blennies along 14 transects, to range from 0.6 to 4.0 individuals/m² (mean = 1.9/m²).

FIGURE 21

NUMBER OF REDLIP BLENNIES IN TRANSECT A VS. TIME (1980-81)

(*) indicates Hurricane Allen



In 1981, the population was at its lowest level ever between February and April, 1981 (Fig. 21). However a definite increase occurred during spring and summer, so that by August 1981, the population was at a level slightly above that of the previous year (1.90 vs. 1.67 fish/m²).

Similar findings were obtained from the second transect (transect B). Figure 22 reveals the same trend operating from February to August 1981. Unfortunately, this transect was not monitored long enough to see the population stabilize at a certain density as in transect A.

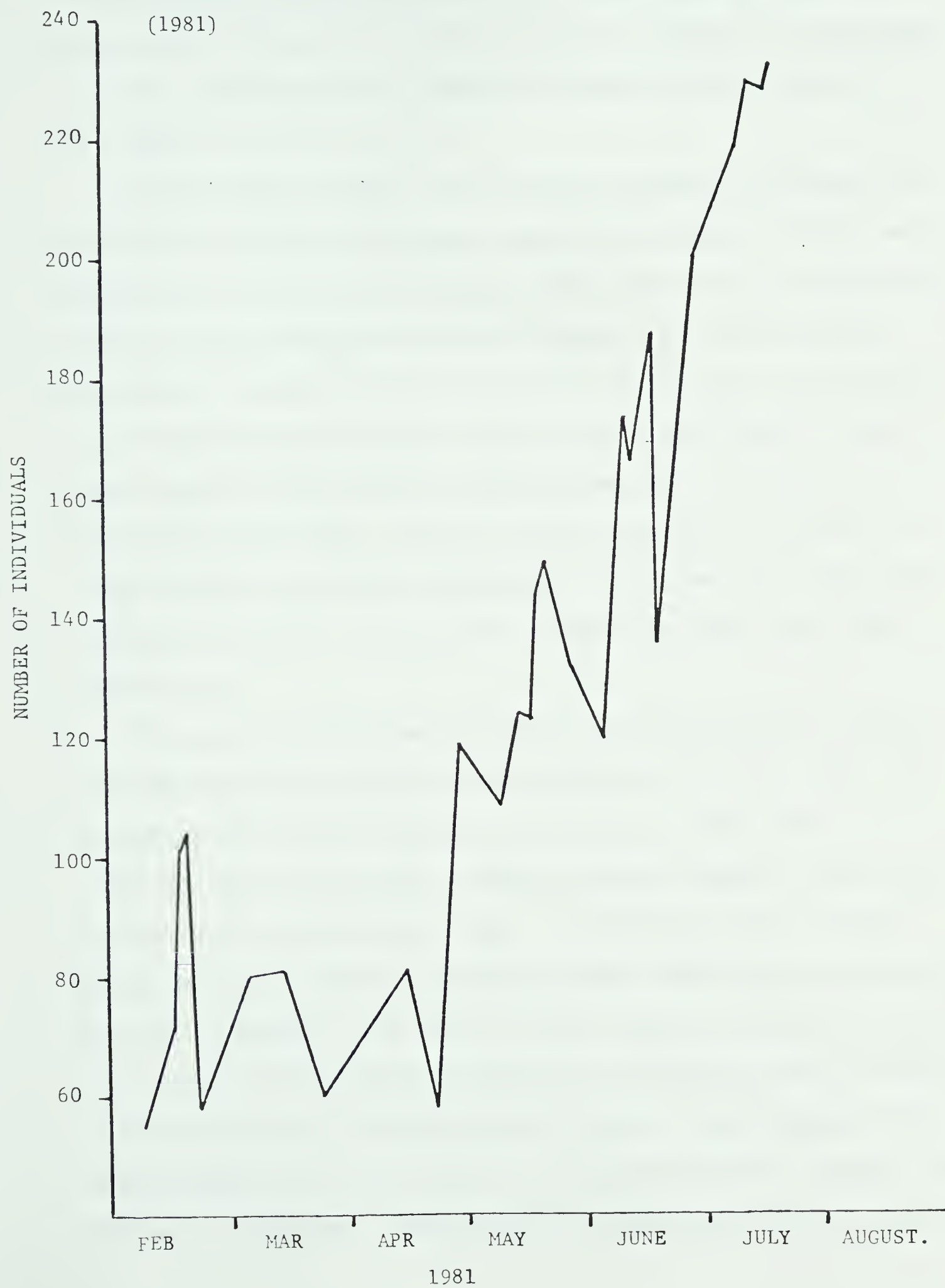
10.3 DISCUSSION

Evidence provided above indicates that the low level of abundance recorded in both transects during the early part of 1981 is not normal. This opinion, based on data from transect A, stems from the fact that the population level during May, 1980, was similar to that of August 1980. One would expect such stability to occur during the 1981 season also.

Such catastrophic decline in the abundance of fishes was probably caused by Hurricane Allen, which hit Barbados on August 3, 1980. The hurricane caused extensive damage to the shoreline of Barbados and to its fringing reefs. Large pieces of coral, protruding from the reefs, were broken off and carried away by the strong currents generated nearshore. Further observations suggested that large amounts of

FIGURE 22

NUMBER OF REDLIP BLENNIES IN TRANSECT B VS. TIME



sediment transported by currents had a "sandblasting" effect on the reefs, destroying the coralline algae on this substrate. A detailed account of other effects of Hurricane Allen on Jamaican coral reefs has been reported (Woody et al. 1981).

Field observations taken during the week following the hurricane revealed that many species of inshore fishes were behaving in an abnormal manner. Most territorial fishes were seen reestablishing territorial boundaries, while others were acquiring the territories of fishes lost in the storm. Many fishes showed severe cuts on their body, while others were seen with sea urchin spines embedded in their skin. Moray eels and other predators were observed in unusually large numbers, possibly attracted by injured prey or by the presence of other fishes still unfamiliar with their new territories.

The exact mechanism by which the population of redlip blennies was decimated is still unclear. The fact that the abundance of redlip blennies in transect A was not drastically reduced after the hurricane, suggests that adult mortality was not severe (Fig. 21). Monthly peaks in the number of individuals observed in May, June and July are not present in August. The lack of such a peak (believed to be a function of recruitment) cannot be attributed with certainty to the effects of the hurricane, since it has already been established that recruitment is disrupted during August (see chapter 9). However, the possibility remains that the pool

of larvae available for recruitment during the period succeeding the month of August may have been washed away. This would have the effect of decreasing the population level to a considerable extent thereafter.

Damage to the reef itself may also have had detrimental effects on the population level. The potential loss of shelters may have caused some redlip blennies to become particularly susceptible to predation pressures. Other blennies re-establishing new territories, are more vulnerable to predation than those already holding permanent territories. All blennies transported away from their original territories would therefore have suffered higher mortality.

Elimination of the food supply must be considered as a serious factor influencing the population size. Woody et al. (1981) reported that during hurricane Allen, the algal lawns defended by damselfishes were eliminated on the West Fore Reef of Jamaica, at depths shallower than 10 m, and were partially disrupted elsewhere. Randall (1967) estimated that blennies ingest cells of 17 species of algae, and that 76.5% of the algal types consumed by the redlip blenny are also consumed by either the dusky damselfish or by the yellowtail damselfish. Although there is no firm evidence indicating that coralline algae was also destroyed in Barbados during the hurricane, this possibility remains to be disproved. If the algae were damaged, it would certainly induce a certain degree of starvation, which in turn can translate into a

reduction of fecundity.

The pattern of abundance observed during the survey cannot be attributed entirely to the effects of the hurricane. Fecundity in *O.atlanticus* has been shown to be decrease during fall and early winter period. This factor may potentially induce a a reduction in population size during the succeeding period. One of the objectives of this survey was to establish the magnitude of the induced fluctuations in population densities. However, due to relatively abnormal circumstances (drastic decline in population size), no comments can be made on this issue.

Sale (1980) reported evidence that tropical fish populations can fluctuate considerably over the long run (28 months). He showed the number of fishes on a patch of reef to vary from 1.5 to 2.3 times between censuses taken at 9 month intervals. Numbers of species varied from 1.2 to 1.6 times during the same interval. He attributed this variation to the fact that assemblages are built up through fluctuations in recruitment of individuals from a large pool of larvae.

Evidence obtained during this survey supports the notion that the population level is influenced by the recruitment of individuals. It appears that the redlip blenny population is well adapted to withstand catastrophic mortality and still regain its original abundance after a few months. This fact would tend to support the view of Smith & Tyler (1972) that there is constancy in faunal

composition and numbers of fish in coral reef communities. I believe that disagreement on this last issue (Sale 1977) lies in failure to recognize that some species are highly specialized to maintain their numerical abundance, while others are not. Conflicting theories can be resolved by conducting further studies on the biology of reef fishes in order to understand the life history traits of members of different communities.

11. CONCLUSION

Several aspects of the life history and behavioral ecology of the redlip blenny have already been investigated (Springer 1962, Nursall 1977, 1981, Marraro 1978). My purpose was to supplement these previous investigations and provide some basic information on the population dynamics of this primary consumer.

Nursall (1977) described territoriality in the redlip blenny. Several other behavioral aspects, including reproductive behavior, were reported by Marraro (1978). The information provided from these preliminary investigations, and in the present study indicate that the reproductive behavior of the redlip blenny resembles that of other tropical blenniids, and is similar that of other shelter-spawners, as reported by Keenleyside (1979). Gibson (1969) noted great similarity in the general pattern of reproductive behavior in different species of shore fishes. The author concluded that such similarity arose through convergent evolution in response to the same selection pressures. I also share Gibson's view that some differences in the reproductive behavior of different species have evolved as ethological isolating mechanisms.

The reef crest zone occupied by *O.atlanticus* is characterized by fluctuations in salinity, temperature, current velocity and turbidity. Furthermore, predation pressures operating in such areas in the tropics can be considered the principal biological factor determining the

survival of the eggs. Selective mate choice, parental care, short incubation period and the periodicity of spawning and hatching probably arose to counteract the harshness of the habitat and to ensure maximal survival of the progeny. It is generally assumed that the fitness of offsprings increases in relation to the energy invested in them (Pianka 1970). However, the intense predation and competition pressures operating in tropical communities have forced most species of tropical marine fishes to opt for the quantity of offspring produced, over their quality (Johannes 1978). It appears that redlip blennies also follow the same rule in this regard.

Embryogenesis in *O.atlanticus* parallels that of other blennies reported in the literature, although its incubation time (96-100h at 29°C.) is one of the shortest reported. Larval morphology is similar to that of other blenniid larvae. Larval blenniids of temperate latitudes possess larger yolk reserves than tropical blenniids, thus redlip blenny larvae initiate feeding at a relatively early stage of development. The planktonic phase of most shore fishes lasts about two months (Gibson 1969). In this regard, *O.atlanticus* larvae do not differ greatly from other species of shore fishes and other blenniids. The growth rate of *O.atlanticus* larvae, during this period, is comparable to that of other known tropical fish larvae, but is faster than those of known blenniid larvae of temperate latitudes, as calculated from data by Stephens et al. (1970).

Coastal waters of the tropics are warmer and more productive than those of temperate latitudes. Behavioral adaptations allow redlip blenny larvae to remain in such areas and to benefit from conditions permitting relatively high growth rates. However, atmospheric and hydrographic conditions existing around islands such as Barbados can also affect the distribution of larvae and thus play an important role in recruitment. Major differences occur between the recruitment patterns of the redlip blenny and of other tropical fishes. Luckhurst & Luckhurst (1976) observed two peaks in recruitment in most species of coral reef fishes, one in spring (March-May), and one in fall (September-November). Peak recruitment of *O.atlanticus* larvae in Barbados occurs during mid-summer, and is influenced by the seasonal spawning pattern of *O.atlanticus*. It is still unclear why redlip blennies have evolved life history traits differing from those of many other tropical fishes. Wourms & Bayne (1973) noted that the fall peak in reproductive activity of the brotulid, *Dinematchthys ilucoetoides*, corresponds to a period of calm between the two annual monsoon seasons. Johannes (1978) noted that throughout the tropics, shallow-water marine fishes have adapted reproductive strategies reducing the transport of larvae offshore, and thus improving their chances of encountering shallow water. Hydrographic and atmospheric conditions at Barbados are relatively stable throughout the year. However the atmospheric and nearshore hydrographic conditions are most

calm during early summer, at the time of peak recruitment of *O. atlanticus* larvae. I believe the redlip blenny population at Barbados is maintained through the recruitment of larvae produced at the island itself. These fish are adapted to maximize their chances of recruitment by having a spawning pattern which reduces the chance of drift mortality. It would appear that other species are not so adapted to benefitting from local hydrographic conditions. It is hypothesized that their pelagic stages may be more susceptible to different kinds of selective pressures. It remains to be proved whether blennioid populations of other islands have identical life history traits. The islands themselves have important effects on the oceanic environment by modifying currents, vertical water movement, wave height, primary productivity and zooplankton composition (Powles 1976). Little information is available on the effects of the geographical and geomorphological attributes of islands upon the retention of larval stocks. Evidence obtained during this study underlines the need for further investigation on such issues. Munro et al. (1973) noted that management strategies for fish populations of Caribbean islands and banks will depend on knowledge of the recruitment mechanisms of these populations, and in particular, on whether recruitment is from local populations or from those further upcurrent.

12. LITERATURE CITED

- Ahlstrom, E.H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wild. Serv. Fish Bull. 60:107-146.
- Allen, G.R. 1972. The Anemonefishes. T.F.H. Publications. Neptune city, N.J. 288pp.
- Bagenal, T.B. 1966. The ecological and geographical aspects of the fecundity of the plaice. J. Mar. Biol. Ass. U.K. 46: 161-186.
- Bagenal, T.B. 1978. Aspects of fish fecundity. Ch.4 in Ecology of Freshwater Fish Production By Gerking, S.D. (ed.), John Wiley & Son. 1978.
- Ballontin, F. & R. Perez 1979. Modalidad de postura, huevos y estados larvales de *Hypsoblennius sordidus* (Bennett) en la bahia de Valparaíso (Blenniidae: Perciformes). Rev. Biol. Mar. Dep. Oceanol. Univ. Chile 16(3):311-318.
- Battle, H.I. 1944. The embryology of the Atlantic salmon, *Salmo salar* (L.). Can. J. Res. D22, 105-125.
- Bishai, H.M. 1960. The effect of hydrogen ion concentration on the survival and distribution of the larval and young fish. Z. Wiss. Zool. 164(1-2):107-108.
- Breder, C.M. Jr. 1941. On the reproductive behavior of the sponge blenny, *Paraclinus marmoratus* (Steindachner). Zoologica 26:233-235 3p.
- Blaxter, J.H.S. 1969. Development of eggs and larvae. In Fish Physiology, W.S. Hoar and D.J. Randall (ed.). Academic Press, New-York. 1969.
- Blaxter, J.H.S. & G. Hempel. 1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons Int. Expl. Mer. 28, 211-40.
- Bohlke, J.E. and C.C.G. Chaplin. 1968. Fishes of the Bahamas and Adjacent Tropical Waters. Livingstone Publishing Co. Wynnewood, PA. 771pp.
- Cassie, R.M. 1968. Sample design. In Zooplankton Sampling by D.J. Tranter (ed.) Unesco, Paris. pp 105-122.
- Cassie, R.M. 1962. Frequency distribution models in the ecology of plankton and other organisms. J. Anim. Ecol. 31: 65-92.

- Childerhose, R.J. & M. Trim. 1979. Pacific Salmon and Steelhead trout. Douglas & McIntyre. Vancouver. 1979.
- Colin, P.L. 1974. Comparative biology of the gobies of the genus *Gobiosoma*, subgenus *Elacatinus*, in the western North Atlantic. Ph.D thesis, Univ. of Miami.
- Conlon, D.M. 1973. Barbados sea-air land exp. Interim Report Coastal Studies Inst. Louisiana State U.
- Connell, J.H., and E. Orians. 1964. The ecological regulation of species diversity. Amer. Nat. 98:399-414.
- Cushing, D.H. 1976. Biology of fishes in the pelagic community. Chapter 13 in The Ecology of the Seas, D.H. Cushing & J.J. Walsh (ed.). W.B. Saunders Co. Toronto. 467pp.
- Davies, N.B. and T.R. Halliday. 1977. Optimal mate selection in the toad *Bufo bufo*. Nature 269: 56-58.
- De Silva 1973. Aspects of the reproductive biology of the sprat, *Sprattus sprattus* (L.), in inshore waters of the west coast of Scotland. J. Fish Biol. 5:689-705.
- Dobzhansky, T. 1950. Evolution in the tropics. Amer. Sci. 38:209-221.
- Dunbar, M.J. 1960. The evolution of stability in marine environments. Natural selection at the ecosystem level. Amer. Nat. 94:129-136.
- Ehrlich, P.R. 1975. The population biology of coral reef fishes. Ann. Rev. Ecol. Syst. 6:211-247.
- Emery, A.R. 1964. The ecological effects of current patterns around islands with special reference to Barbados. M.Sc. Thesis, McGill University, Montreal, Canada.
- Emery, A.R. 1968. Comparative ecology of damselfishes (Pisces:Pomacentridae) at Aligator Reef, Florida Keys. Ph.D thesis, University of Miami Florida. 258pp.
- Emery, A.R. 1972. Eddy formation from an oceanic island: ecological effects. Carib. J. Sci. 12(3-4):121-128.
- Erdman, D.S. 1957. Recent fish records from Puerto Rico. Bull. Mar. Sci. Gulf. Carib. 6:315-340.
- Erdman, D.S. 1976. Spawning patterns of fish from Northeastern Caribbean. In Symposium on Progress in the Caribbean and Adjacent Regions. pp145-170. Caracas 1976. FAO Fish Report #200.

- Fishelson, L. 1976. Spawning and larval development of the Blennioid fish, *Melacanthus nigrolineatus*, from the red sea. *Copeia* 4:798-800
- Fisher, A.G. 1960. Latitudinal variations in organic diversity. *Evolution* 14:64-81.
- Fisher, W. (ed.). 1978. FAO Species Identification Sheets. Western central Atlantic (fishing area 31). Vol. 1-7. FAO, Rome, Italy.
- Fives, J.M. 1980. An account of the eggs and developmental stages of Montagu's Blenny, *Coryphoblennius galerita* (L.), with notes on the reproductive behavior of the adults. *J. Mar. Biol. Ass. U.K.* 60,749-757.
- Halliday, T.R. 1978. Sexual selection and mate choice. Chapter 7 in *Behavioral Ecology, an Evolutionary Approach*, J.R. Krebs and N.B. Davies (ed.). Blackwell Scientific Publ. London, England.
- Harden Jones, F.R. 1968. *Fish Migrations*. Edward Arnold, London. 325pp.
- Hildebrand, A.F. & L.E. Cable. 1938. Further notes on the development and life history of some teleosts at Beaufort, N.C. U.S. Bur. Fish Bull. 24: 505-642
- Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe. *ICES Rapp. et Proc. Verb.* 20: 238pp.
- Hobson, E.S. 1974. Feeding relationship of teleostean fishes on coral reefs in Kona, Hawaii U.S. Fish Bull 72:915-1031.
- Hobson, E.S. & J.R. Chess. 1978. Trophic relationships among fishes and plankton at Enewetak. U.S. Fish Bull. 76(1).
- Houde, E.D. & B.J. Palko. 1970. Laboratory rearing of the clupeid fish *Harengula pensacolatae* from fertilized eggs. *Mar. Biol.* 5:354-358.
- Huxley, J.S. 1938. The present standing of the theory of sexual selection. *The Clarendon Press*, G.R. De Beer (ed.). pp11-42.
- Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Env. Biol. Fish.* Vol 3, no 1, pp.65-84.
- Johannes, R.E. & R. Gerber. 1974. Import and export of detritus and zooplankton by an Eniwetok coral reef community *Proc. 2nd Int. Symp. Coral Reefs.* 1:97-104.

- Keenleyside, M.M.A. 1979. Diversity and adaptation in Fish Behavior. Springer-Verlag, Berlin 1979, 208pp.
- Kotrschal, K. & A. Goldschmid. 1981. Population structure of *Blennius incognitus*, Bath 1968 (Pisces: Teleostei: Blenniidae) during the reproductive period with comments on age & growth of small benthic littoral fishes. Marine Ecology, 2:1-16.
- Leis, J.M. & J.M. Miller. 1976. Offshore distribution patterns of Hawaiian fish larvae. Marine Biology 36, 359-367.
- Lewis, J.B. 1960. The coral reefs and coral communities of Barbados, W.I. Can J. Zool. 38:1133-1145.
- Lewis, J.B., et al. 1962. The biology of the flying fish *Hirundichthys affinis* (Gunther). Bull. Mar. Sci. Gulf. Caribb. 12:73-94.
- Lewis, J.B. & A.G. Fish. 1969. Seasonal variation of the zooplankton fauna waters entering the Caribbean Sea at Barbados. Caribb. J. Sci. 9: 1-24.
- Lippson, A.J. and R.L. Moran. 1974. Manual for identification of early development stages of fishes of the Potomac estuary. Md. Dept. Nat. Res. Power Plant Siting Program. PPSP-MP-13 282pp.
- Lobel, P.S. 1978. Diel, lunar and seasonal periodicity in the reproductive behavior of the pomacanthid fish, *Centropyge potteri*, and some other reef fishes. Pacific Sci 32:193-207.
- Luckhurst, B.E. and K. Luckhurst. 1977. Recruitment patterns of coral reef fishes on the fringing reef of Curacao, Netherlands, Antilles. Can. J. Zool. 55:681-689.
- MacArthur, R.H. 1965. Patterns of species diversity. Biol Rev. 40:510-533.
- Marliave, J.B. 1976. Behavioral transformations of planktonic larvae. Ph.D. Thesis, University of British Columbia. Vancouver, Canada.
- Marliave, J.B. (no date) Laboratory rearing of Marine fish larvae. Vancouver Public Aquarium Manuscript, Vancouver.
- Marliave, J.B. 1977. Development of behavior in marine fish. Memorial University. Mar. Sci. Res. Lab. Tech. Rep. 1977. pp.240-266.
- Marraro, C.H. 1978. Some aspects of the life history and behavioral ecology of the redlip blenny, *Ophioblennius*

- atlanticus*. M.Sc. Thesis, University of Alberta. Edmonton, Canada. 196pp.
- Marshall, N.B. 1963. The Life of Fishes. World Publishing Co. Cleveland, U.S.A. 402 pp.
- Miller, J.M. 1973. Nearshore distribution of Hawaiian marine fish larvae: effects of water quality, turbidity and currents. In The Early life History of Fishes, J.H.S. Blaxter (ed.) Springer Verlag (1974). New-York pp.217-231
- Miller, J.M. 1979. Nearshore abundance of tuna (Pisces: Scombridae) larvae in the Hawaiian Islands Bull. Mar. Sci. 29(1): 19-26, 1979.
- Moore, U. and F. Sander. 1977. A study of the offshore zooplankton of the tropical western atlantic near Barbados. Ophelia, 16(1),77-96.
- Munro, J.L. 1976. Actual and potential fish production from the coralline shelves of the Caribbean sea. In Symposium on progress in Marine Research in the Caribbean and adjacent regions. FAO Fisheries Report #200. pp.301-333. Caracas 1976.
- Munro, J.L., V.C. Gaut, R. Thompson & P.H. Reeson. 1973. The spawning seasons of the Caribbean reef fishes. J. Fish. Biol. 5:69-84.
- Murray, P.M., H.H. Roberts, D.M. Conlon, G.M. Rudder. 1977. Nearshore current fields around coral islands: control on sediment accumulation and reef growth. Proceedings 3rd Int. Coral Reef Symp. pp.53-59.
- Nursall, J.R. 1977. Territoriality in Redlip blennies, *Ophioblennius atlanticus* (Pisces: Blenniidae). J. Zool. Lond. 182:205-223.
- Nursall, J.R. 1981. The activity budget and use of territory by a tropical blennioid fish. Zool. Jour. Linn. Soc. 72:69-92.
- Ott, B. 1975. Community patterns on a submerged barrier reef at Barbados, West Indies. Rev. Ges. Hydrobiol. 60:6 pp.719-736.
- Paine, R.T. 1966. Food web complexity and species diversity. Amer. Nat. 100:65-75.
- Peck, G.S. 1978. A physical oceanography study of the southwestern coast of Barbados. M.Sc thesis. McGill University, Montreal, Canada. 1978.

- Peters, K.M. 1981. Reproductive biology and developmental osteology of the florida blenny, *Chasmodes saburnae* (Perciformes: Blenniidae). North. Gulf Sci. 4(2):79-98.
- Pianka, E.R. 1970. On r and k selection. Am. Natur. 104:592-597.
- Powles, H. 1975. Abundance, seasonality, distribution and aspects of the ecology of some larval fishes off Barbados. Ph.D. Thesis, Marine Sciences Center, McGill University. Montreal Canada. 1975.
- Powles, H. 1976. Island mass effects on the distribution of two pelagic fish species off Barbados. Symposium on progress in marine research in the Caribbean and adjacent regions. FAO Fisheries Report 200:333-346.
- Pressley, P.H. 1980. Lunar periodicity in the spawning of the yellowtail damselfish, *Microspathodon chrysurus*. Env. Biol. Fish. 5(2):153-159.
- Qasim, S.Z. 1955. Time and duration of spawning season of teleosts in relation to their distribution. J. Cons. Inter. Explor. Mer. 21:144-145.
- Ralston, S. 1976. Age determination of tropical reef butterflyfish, utilizing daily growth rings of otoliths. U.S Fish. Bull. 74:690-695.
- Randall, J.E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. Miami. 5:665-847.
- Randall, J.E. 1968. Caribbean Reef Fishes. T.F.H. Publications Inc. Neptune City, N.J. 318pp.
- Randall, J.E. and H.A. Randall 1963. The spawning and early development of the atlantic parrotfish, *Sparisoma rubripinne*, with notes on other scarids and labrisomid fishes. Zoologica 48:49-60.
- Raymont, J.E. 1963. Plankton Productivity in the Oceans. Pergamon Press. Oxford. 600pp.
- Raymont, J.E. 1966. The production of marine plankton. Adv. Ecol. Res. 3:117-191.
- Razniewski, J. 1970. On the occurrence of spawning concentrations of some fish species over the Northwest African Shelf in the summer of 1967. Rapport. P.V. Reun. Cons. Perm. Int. Expl. Mer. 159:199-201.
- Rice, A.L. 1964. Observation on the effects of changes of hydrostatic pressure on the behavior of some marine animals. J. Mar. Biol. Ass. U.K. 44:163-175.

- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. J. Fish. Res. Board. Can. 191:1-382.
- Ricker, W.E. 1973. Linear regression in fishery research. J. Fish. Res. Board. 30:409-434.
- Ross, R.M. 1978. Reproductive behavior of the anemonefish *Amphiprion melanopus* on Guam. Copeia. 1978. 1:103-107.
- Rounsefell, G.A. 1957. Fecundity of the North American Salmonidae. U.S. Fish. Wild. Serv. Fish. Bull. 57(122):451-468.
- Russell, B.C., F.H. Talbot & S. Domm. 1974. Patterns of colonization of artificial reefs by coral reef fishes. Proc. Second. Int. Symp. Coral Reefs. 1:207-215.
- Russell, F.S. 1976. The eggs and planktonic stages of British marine fishes. Academic Press, London. 524pp.
- Ryland, J.S. 1963. The swimming speeds of plaice larvae. J. Exp. Biol. 40:285-299.
- Ryther, J.H., D.W. Menzel and N. Corwin. 1967. The influence of the Amazon River outflow on the ecology of the Western tropical Atlantic. J. Mar. Res. 25:69-83.
- Sale, P.F. 1974. Mechanisms of coexistence in a guild of territorial fishes at Heron Island. Proc. Second Int. Coral. Reef Symp. Cameron et al (eds). Great Barrier Reef Comm. Brisbane, Queensland, Australia. pp.82-95.
- Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. Amer. Nat. 111(978):337-359.
- Sale, P.F. 1980. Assemblages of fish on patch reefs- Predictable or unpredictable? Env. Biol. Fish. 5(3):243-249.
- Sale, P.F., P.J. Doherty, W.A. Douglas. 1980. Juvenile recruitment strategies and coexistence of territorial pomacentrid fishes. Bull. Mar. Sci. 30:147-158.
- Sale, P.F. and R. Dybdhal. 1975. Determinants of community structure for coral reef fishes in an experimental habitat. Ecology, 56:1343-1355.
- Sander, F. and D.M. Steven. 1973. Organic productivity of inshore and offshore waters of Barbados. Bull. of Mar. Science. 23(4)771-792 .
- Saksena, V.P. & E.D. Houde. 1972. Effects of food level on the growth and survival of laboratory reared larvae of

- bay anchovy, *Anchoa mitchilli* (Valenciennes), and scaled sardine *Harengula pensacolata* (Goode & Beane), J. Exp. Mar. Biol. Eco. 8:249-258.
- Scott, J. 1961. Effects of food quantity on fecundity of the rainbow trout *Salmo gairdneri* J. Fish. Res. Board Can. 19, 715-731.
- Shackley, S.E. and P.E. King. 1978. A sterile sea water circulating system for the jar culture of developing fish eggs. J. Fish. Biol. 12:235-237.
- Shirota, A. 1970. Studies on the mouth size of fish larvae. Bull. Jap. Soc. Fish 36:353-368. (In Japanese with English abstract).
- Slobodkin, L.B. and H.L. Sanders 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. 22:82-93.
- Smith, C.L. and J.C. Tyler. 1972. Space resource sharing in a coral reef fish community. Bull. Nat. Hist. Mus. Los Angeles. Co. 14:125-170.
- Smith, P.E. & S.L. Richardson. 1977. Standard techniques for pelagic fish eggs and larval surveys. FAO fisheries technical papers no 175. FAO, Rome, Italy. December 1977.
- Snyder, D.E. 1981. Contributions to a guide to the Cypriniform fish larvae of the upper Colorado river system in Colorado. United States Bureau of Land Management. Denver, Colorado. 81pp.
- Springer, V.G. 1962. A review of blennioid fishes of the genus *Ophioblennius* (Gill.). Copeia 2:426-433.
- Stephens, J.S. Jr., R.K. Johnson, G.S. Key, J.E. McCosker. 1970. The comparative ecology three sympatric species of California blennies of the genus *Hypsoblennius* Gill (Teleostomi, Blenniidae). Ecol. Mon. 40:213-233.
- Steven, D.M. 1971. Primary productivity of the tropical western Atlantic Ocean near Barbados. Mar. Biol. 10:261-264.
- Steven, D.M., A.L. Brooks and E.A. Moore. 1970. Primary and secondary production in the tropical Atlantic. Bermuda Biological Station, Final Report.
- Steven, D.M. and Brooks, A.L. 1972. Identification of Amazon river water at Barbados, West-Indies, by salinity and silicate measurements. Marine Biology 14, 345-348.

- Stevenson, D.K. & N. Marshall. 1974. Generalizations of the fisheries of coral reefs and adjacent shallow-water environments. Proceedings of the Second International Coral Reef Symposium 1. pp. 147-156.
- Thompson, R. and J.L. Munro. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae. J. Fish. Biol. 1978, 12:115-146.
- Trivers, R.L. 1972. Parental investment and sexual selection. In Sexual Selection and the Descent of Man. B. Campbell (ed.), Aldine. Chicago. U.S.A.
- Ursin, E. 1973. On the prey-size preference of cod and dab. Medd. Danm. Fisk.-og Havunders. N.S. 7:85-98.
- Wallace, A.R. 1878. Tropical Nature and Other Essays. McMillan, New-York.
- Watson, W. and J. Leis. 1974. Ichthyoplankton of Kanehoe Bay, Hawaii: A one year study of fish eggs and larvae. University of Hawaii Sea Grant Program, Honolulu Technical Report. 75-1.
- Warner, R.R. 1975. Life history of *Pimelometopon pulchrum*, Pisces: Labridae. Fish. Bull. 73:262-283.
- Woodley, J.D. et al. 1981. Hurricane Allen's Impact on Jamaican coral reefs. Science, 214(4522):749-755.
- Wourms, J.P. & O. Bayne. 1973. Development of the viviparous brotulid fish, *Dinematichthys ilucoeteoides*. Copeia 1:32-40.
- Wourms, J.P. & D. Evans 1974. The embryonic development of the black prickleback, *Xiphister atropurpureus*, a Pacific Coast blennoid fish. Can. J. Zool. 52:879-887.
- Wust, G. 1964. Stratification and circulation in the Antilles of the Caribbean Basin. Columbia Univ. Press. N.Y. 201.
- Wyatt, T. 1972. Some effects of food density on the growth and behavior of plaice larvae. Mar. Biol. 14:210-216.

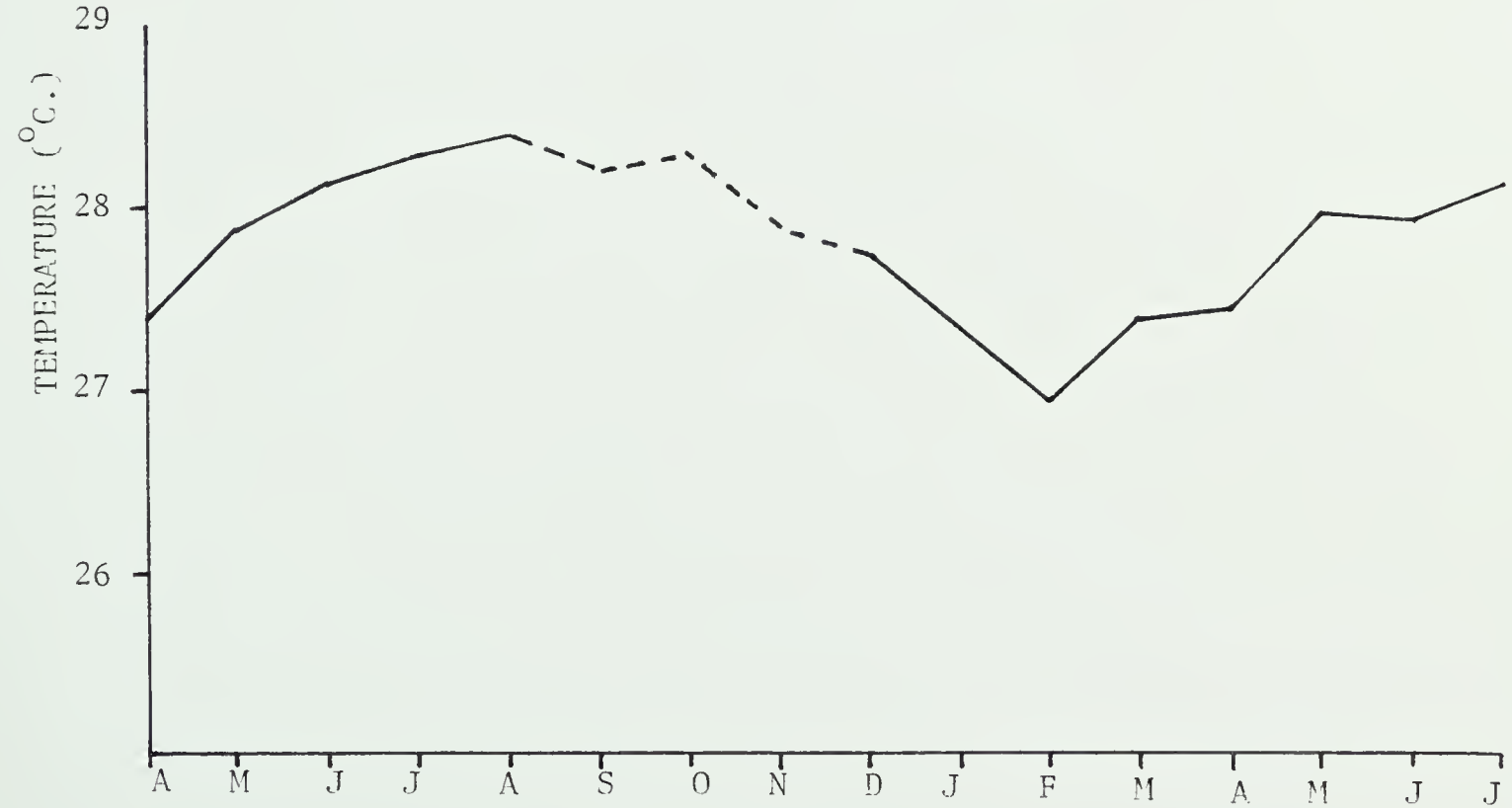
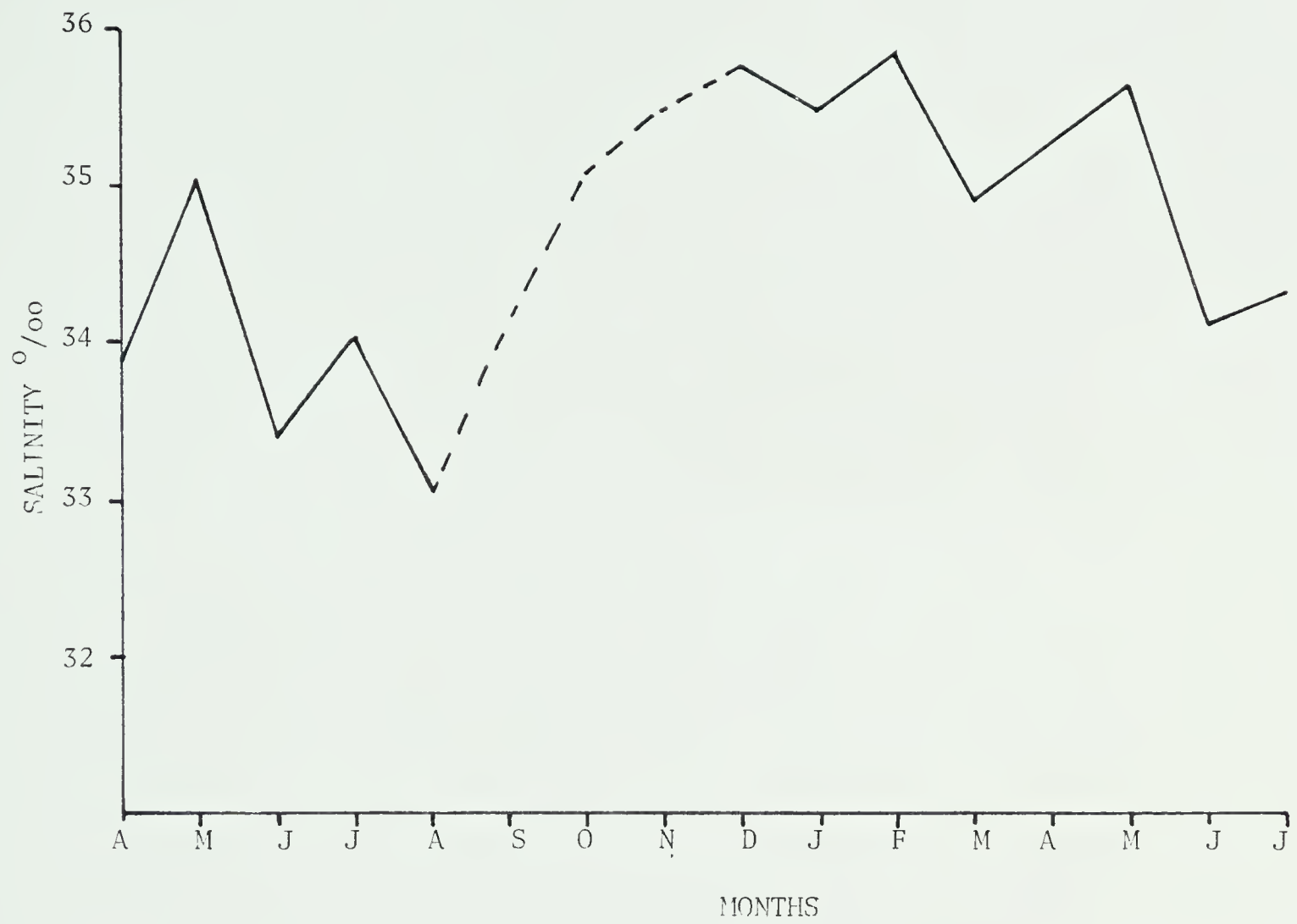
13. APPENDIX

FIGURE 23

Salinity and temperature profile of surface waters at
Barbados (1980-1981)

Data from Dr. M. Spindler.

Estimated values from Sander & Steven (1973).



B30349